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Renewable Resource Production Surfaces, Bioeconomic Steady States, and Space

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Abstract

This paper explores production surfaces for a spatially differentiated renewable resource. By analyzing steady state harvests for a fixed amount of total harvesting effort, the conceptual model evaluates management using protected areas and assesses the importance of assumptions about spatial behavior. A simulation of marine reserves with Beverton-Holt recruitment is presented.

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I. Introduction

Resource scientists have recently shown substantial support for managing fisheries with marine protected areas, signifying a new resource management paradigm that recognizes the importance of spatial processes in both untouched and exploited systems. Numerous biological studies argue that marine reserves, or no-take zones, could benefit fishery management (Davis, 1989; Polacheck, 1990; Roberts and Polunin, 1991, 1993; Bohnsack, 1993, 1998; Carr and Reed, 1993; DeMartini, 1993; Dugan and Davis, 1993; Quinn et al., 1993; Man et al., 1995; Clark, 1996; Russ and Alcala, 1996; Lauck et al., 1998; Guenette and Pitcher, 1999; Hastings and Botsford, 1999; Mangel, 2000; Walters, 2000).¹ While scientists have put forward a number of reasons for why spatial management is sensible, arguably the most significant conclusion for the fishing industry is that reserves can generate both conservation benefits and long-term harvest increases.² If this conjecture about reserves is true, then we might expect that over time reserves will become far more palatable in fishing communities. However, many projections of increased fishing yield are overly optimistic because they ignore the spatial heterogeneity of fishing behavior.

Most research that supports the idea that reserves will increase fishing yields is counter-factual policy modeling. That is, researchers build analytical or simulation models that strive to assess what would happen if a reserve were created in a particular (or in some cases a general) fishery. There

¹ Although a complete review of this literature is beyond the scope of this paper, these references are some of the high profile and frequently cited studies on the subject. Two of them (Roberts and Polunin, 1991; Dugan and Davis, 1993) provide reviews of the biological literature on marine reserves.

² Biological analyses of marine reserves outline five interrelated justifications for using marine reserves to manage commercial fisheries. Reserves can rebuild overexploited areas (Polacheck, 1990; DeMartini, 1993; Bohnsack, 1993), take advantage of dispersal mechanisms in boosting system-wide biological production (Davis, 1989; Polacheck, 1990; DeMartini, 1993; Bohnsack, 1993; Carr and Reed, 1993; Lauck et al., 1998), encourage returns to scale and size in system-wide production (Roberts and Polunin, 1991; DeMartini, 1993; Bohnsack, 1993), preserve the natural life cycle of an organism (Polacheck, 1990; Bohnsack, 1993; Carr and Reed, 1993), and provide a hedge

certainly is substantial empirical evidence that supports population recovery within a reserve (Roberts and Polunin, 1991; Dugan and Davis, 1993; Russ and Alcala, 1996). However, there is limited empirical evidence demonstrating that long-term fishing yields increase (McClanahan and Kaunda-Arara, 1995; Roberts et al., 2001).^{3,4} Nevertheless, the idea that reserves will generate fishery benefits in addition to conservation benefits is becoming widely accepted in biological circles. Rather than relying on empirical evidence, the most compelling arguments in favor of reserves have come from biological modeling efforts that show how a reserve can simultaneously increase spawning biomass and fishing yield. A recent National Research Council report on Marine Protected Areas chooses to paraphrase a yet unpublished review of these modeling studies, “with a constant level of effort that would otherwise result in overfishing, models indicate that reserves would increase the yield of the fishery relative to conventional management”(NRC, 2001, p. 143). The overall enthusiasm for reserves and the rapid rise of new policies to promote reserve formation necessitate a careful evaluation of the robustness of these models.

In contrast to the biological literature, economists have shown more skepticism about reserve formation, although they have identified some conditions under which marine reserves will lead to fishery gains for an exploited resource. By extending existing bioeconomic models to space, economists stress that whether a reserve generates net benefits involves a complex function of economic and biological factors (Sanchirico and Wilen, 1999). One immediate economic concern is that the long-term gains from reserve creation, when discounted, may not outweigh short-term costs (Holland and Brazee, 1996; Conrad, 1999). Another key concern is simply that reserves do not address open access rent dissipation forces that are at work in the remaining fished areas (Hannesson, 1998). Even under open access, reserves can generate steady state biomass and harvest increases under some scenarios (Pezzey et al., 2000; Sanchirico and Wilen, 2001). Whether these gains translate into net economic benefits is another

against stock collapses (Bohnsack, 1993; Carr and Reed, 1993; Clark, 1996; Lauck et al., 1998; Hastings and Botsford, 1999). For further discussion of these mechanisms, see Smith, 2001.

³ McClanahan and Kaunda-Arara actually found that total catch decreased, although catch per unit effort increased with a reserve.

question, and the only study that demonstrates that implementing a reserve is the optimal policy relies heavily on a strong biological assumption of a common larval pool (Brown and Roughgarden, 1997). The only empirically based bioeconomic model of reserves suggests that not only do economic net benefits fail to materialize but also that long-term harvest predictions are lower than management without reserves (Smith and Wilen, 2002).

This paper helps to reconcile marine reserve promotion by biologists with the skepticism of economists by recasting the biological modeling literature into production economics and exploring production surfaces for a spatially differentiated renewable resource. A conceptual framework is constructed to analyze steady state harvests for a fixed amount of total harvesting effort. The resulting model, which applies to a wide range of renewable resource problems, is used to examine management through protected areas and to evaluate the importance of assumptions about spatial behavior. A simulation of marine reserve formation in a fishery with Beverton-Holt recruitment adds larval dispersal to the conceptual framework. Together, these analyses help to explain the divergence between the overwhelming support of biologists and the qualified enthusiasm of resource economists for marine protected areas as a fishery management tool.

Comparing the economic literature on reserves to the biological literature is difficult because numerous factors differ. The introduction of discounting, dynamic (and spatial) behavior, and open access incentives in economic models ultimately means that the modeling works across disciplines are essentially apples and oranges. As such, this paper focuses just on the steady state effect of a reserve on total harvest and assumes, like much of the biological literature, that total fishing effort is fixed before and after reserve creation.

The central argument in this paper is as follows. First, empirically fishing effort is not uniformly distributed across space. Second, steady state production surfaces are non-monotonic in effort. Third, many biological models of a reserve incorporate a non-convexity in the steady state production surface at

⁴ Undoubtedly, the sparseness of empirical support is at least partly due to the sparseness of reserves designed specifically for fishery management, the difficulty of collecting data in these settings, and potentially long time

high levels of exploitation. Fourth, high exploitation rates are the most likely cases in which reserves will be considered. Fifth, in spite of empirical evidence to the contrary, most biological models that evaluate marine reserves assume that fishing effort is uniformly distributed across space. Finally, when spatial management is considered, the non-convexity combined non-monotonicity, high exploitation, and the seemingly innocuous behavioral assumption of spatial uniformity lead to overly optimistic predictions about the potential gains from management with reserves. Thus, the virtually unqualified support of marine biologists for marine reserves as a management tool is partly an artifact of an inaccurate behavioral simplification.

Section II reviews the empirical fisheries and fisheries economics literature to establish that fishing effort is not distributed uniformly across space. Section III defines renewable resource production surfaces and explains the rationale for why they typically are non-monotonic and have non-convexities. Section IV presents a simple but quite general conceptual model with propositions to shed light on the biases in marine reserve modeling. Section V presents a simulation model that accounts for larval dispersal of organisms and demonstrates again that simplifying behavioral assumptions bias results in favor of marine reserves. Finally, section VI discusses the results.

II. Spatial Heterogeneity of Renewable Resource Harvesters

There is substantial evidence that actual commercial fishing is not uniformly distributed across space but rather responds to relative economic incentives. In many circumstances, this leads to a pattern of spatial heterogeneity. Literature in fisheries science analyzes spatial heterogeneity both in attempts to explain differences in fishing power (Hilborn, 1985; Hilborn and Ledbetter, 1985) and in efforts to account for fleet movement (Hilborn and Ledbetter, 1979; Abrahams and Healey, 1990). Several economic papers estimate structural models of fishing location choice that clearly demonstrate how individual commercial fishing decisions respond to relative economic opportunities across space (Eales and Wilen, 1986; Dupont, 1993; Larson et al, 1999; Holland and Sutinen, 2000; Mistiaen and Strand, 2000; Smith, 2002). In some of these studies, a non-uniform pattern of spatial exploitation will persist

horizons required for stock benefits to spill over into fished areas.

even when measurable economic opportunities equilibrate across space because harvesters are heterogeneous or have heterogeneous past experiences.

However, the biological modeling literature cited above primarily assumes uniform behavior.⁵ The key issue at present is whether the behavioral simplification that most conceptual models posit leads to qualitatively different conclusions. The short answer is that this simplification matters a great deal, and qualitative predictions from models are predictably over- or under-optimistic depending on the characteristics of the resource production surface.

III. Steady State Production Surfaces, Non-Monotonicity, and Non-Convexity

In many renewable resource settings, steady state production as a function of effort (harvesting intensity) is non-monotonic, usually due to a combination of intrinsic biological growth and carrying capacity. As steady state effort increases, steady state harvest increases and then decreases. In a typical production setting, one would assume free disposal of effort, and the production function would effectively flatten out at its peak. However, in many renewable resource settings, free disposal is an unreasonable assumption in the steady state as a result of discounting; when there are small or nonexistent stock effects, harvest is decreasing in effort at the optimal steady state stock and harvest. Similarly, harvest is also typically decreasing in effort at the open access steady state stock level. In a heavily exploited fishery for which management with reserves is under consideration, we expect that steady state production is characterized by a place on the back side of this effort/harvest curve.

The most common production model in fisheries economics is the Schaefer (1957) logistic growth model in which net growth in fish stock is a quadratic function of existing stock. Figure 1 depicts this classic textbook starting place for many fisheries economics models. The most common production function for this simple system is one in which harvest is proportional to fishing effort and stock size. With this production relationship, the shape of steady state harvest as a function of effort is parabolic as in Figure 1. Unlike in a static production setting in which we typically assume free disposal of an input,

⁵ One exception is Walters (2000), who builds responsiveness to economic opportunities into his ECOSPACE model.

steady state production of a renewable resource rises, peaks, and then falls as a function of the amount of the input fishing effort. This non-monotonicity of steady state production is a direct consequence of the underlying biological dynamics.

More realistic depictions of biological production in exploited renewable resource systems allow for non-convexities in net growth functions or in harvest functions. A non-convexity means that there exist points outside the production set along a convex combination of two points on the boundary of the set. Such non-convexities can arise due to pure biological compensation, biological depensation, or size limit regulations.⁶ Our focus here is on compensation, since most marine reserve models incorporate compensatory mechanisms. Pure compensation exists when net growth as a proportion of stock is a decreasing function of the stock size (Clark, 1990). The motivation for compensation is density dependent survival at high population levels.

The generalized logistic growth model (Clark, 1990) can account for both compensatory and depensatory mechanisms, which in turn introduce non-convexities in the steady state harvest/effort relationship. Figure 2 depicts a growth curve with pure compensation, and Figure 3 depicts the corresponding effort/harvest curve. The effort/harvest curve is a production surface. It has an inflection point at a high level of exploitation where the production surface changes from a concave to a convex function.

Many conceptual studies of marine reserves use Beverton-Holt yield per recruit models, and indeed Beverton and Holt were the first to consider reserves as a fishery management tool (Guenette et al., 1998). The standard Beverton-Holt stock recruitment function generates pure compensation (Quinn and Deriso, 1999), which in turn creates a non-convexity in the harvest/effort surface. Similarly, fixed size limits in the Beverton-Holt fisheries model also lead to the same form of non-convexity because

⁶ We do not rule out the possibility that production technologies and their interactions with stock levels may also produce non-convexities. For instance, additional search burden for harvesters with a lower stock level could moderate the impact on the stock under increased harvesting pressure. However, the focus in this paper is on biological mechanisms.

fishing effort can only harvest organisms that pass the size limit.⁷ Overall, at high levels of exploitation, i.e. fishing effort levels beyond the maximum sustainable yield, production is decreasing in effort first at an increasing rate and then at a decreasing rate.

Appendix A derives steady state production for a two-patch Beverton-Holt model. Figures 4 and 5 depicts the steady state production surface for two different values of the slope of the stock recruitment function ($a=18$ and $a=40$). The peak of each surface is the steady state maximum sustainable yield and corresponds is characterized by a magnitude and spatial distribution of fishing effort. Here there is neither larval nor adult dispersal, and the biological parameters are the same across patches. Thus, the peak occurs where effort is uniformly distributed.

While production non-convexities can complicate bioeconomic modeling of single pool resources, when space is introduced, the consequences are more severe. As we will see in the next section, the assumed baseline spatial distribution of fishing effort greatly affects the conclusions about total system harvest when creating a reserve.

IV. A Conceptual Model of Steady State Production in Space

Figures 6 and 7 depict level sets for the two production surfaces. Thus, we can view these contours as isoquants. In both figures, we see not only the non-monotonic relationship between f values and production but also the changing shapes of isoquants and how they reflect production set non-convexities. Here it is important to recall that the upper contour sets lie further from the origin for contours before the point of maximum production and closer to the origin for contours beyond the maximum sustainable yield. This figure also reinforces the importance of not assuming free disposal. If we permit free disposal of fishing effort, then the curve never turns down past the maximum sustainable yield.

Figure 8 zooms in on the first level sets, depicts more of the contours, adds several iso-effort lines (lines along which total system-wide effort is constant), and removes the contour labels for clarity. This figure uses a gray scale so that lighter shades correspond to higher elevations on the production surface.

⁷ This assumes knife-edge selectivity.

We will use this figure to evaluate the importance of the distribution of fishing effort and not just the magnitude of effort. The iso-effort lines divide each figure into four regions. First we define these regions. All regions are bounded by the positive orthant. Next we apply Jensen's inequality to prove two simple lemmas. Finally, the results of the analysis are summarized in four propositions. Note that system-wide yield is $y(f_1, f_2)$, or more concisely, $y(\mathbf{f})$. Figure 8 motivates the following definitions of production regions, but it is important to emphasize that these definitions are more general than the analytical model that produced Figures 4-8. The definitions of the production regions are:

Region 1

Production is increasing and strictly concave in \mathbf{f} . The boundary is defined by $(f_1^*, 0)$ and $(0, f_2^*)$ where $f_1^* = \text{argmax}[y(f_1, 0)]$ and $f_2^* = \text{argmax}[y(0, f_2)]$. That is, the boundary is the point on each axis that corresponds to each patch's maximum sustainable yield.

Region 2

Production is strictly concave in \mathbf{f} , increasing for part of the region, and decreasing for part of the region. Along the axes, production is decreasing in f because f 's are beyond patch-specific maximum sustainable yields. The boundary is defined by $(f_1^{**} + f_2^{**}, 0)$ and $(0, f_1^{**} + f_2^{**})$, where $[f_1^{**}, f_2^{**}] = \text{argmax}[y(\mathbf{f})]$. That is, the boundary is the point on each axis that corresponds to the total amount of fishing effort at the system-wide maximum sustainable yield.

Region 3

Production is decreasing and strictly concave in \mathbf{f} . The boundary is defined by the plane of inflection between the convex and concave region of the production surface.⁸

Region 4

Production is decreasing and strictly convex in \mathbf{f} .

In the following two lemmas, we appeal to Jensen's Inequality rather than simply apply the definitions of concave and convex functions. The reason is to present results that are proved easily but generalize to more complicated settings including a larger number of patches and fishing distributions that are continuous across space.

Lemma 1

A uniform distribution of fishing effort maximizes system-wide production in regions 1, 2, and 3.

⁸ In Figure 8, the plane depicted is linear, but it in general it does not have to be linear.

Proof: $Y^{\text{tot}} = y(f_1) + y(f_2) = 2 \cdot E[y(\mathbf{f})]$. For a uniform distribution of effort, $Y^{\text{tot}} = y((f_1+f_2)/2) + y((f_1+f_2)/2) = 2y(E[\mathbf{f}])$. By Jensen's Inequality, $y(E[\mathbf{f}]) \geq E[y(\mathbf{f})]$. Q.E.D.

Lemma 2

A uniform distribution of fishing effort minimizes system-wide production in region 4.

Proof: Same as Lemma 1 except using the result from Jensen's Inequality for convex functions.

Proposition 1

For a given isoquant in region 1, a redistribution of uniform fishing effort into a reserve allocation decreases production **more** than the same redistribution of any other effort allocation along the same isoquant.

Proof: A reserve allocation corresponds to a point on either axis. By definition, yield is increasing in either f throughout region 1. Since uniform effort maximizes production for a given total effort (from Lemma 1), it has a dual interpretation as the minimum effort needed to obtain a given yield. Thus all other effort allocations for that yield correspond to a higher iso-effort line. The higher iso-effort line intersects the axes further from the origin, i.e. at a higher production level, than the iso-effort line corresponding to the uniform distribution of effort. Q.E.D.

The immediate implication of Proposition 1 is that at low levels of exploitation a reserve is likely to seem worse in terms of system-wide steady state harvest than it really is. That is, if analysts assume uniform fishing effort when, in fact, effort is heterogeneous across space, a reserve will appear to be a less favorable option than it really is under the correct effort distribution assumption.

Proposition 2

For a given isoquant in region 2, a redistribution of uniform fishing effort into a reserve allocation decreases production **less** than the same redistribution of any other effort allocation along the same isoquant.

Proof: The proof is the same as the proof for proposition 1, and we note simply that by definition of region 2, points along the axes correspond to lower levels of production as they move further from the origin.

The implication of Proposition 2 is just the opposite of Proposition 1. If managers falsely assume uniform effort, they will infer that reserves are less costly in terms of total yield than they actually are.

Proposition 3

For a given isoquant in region 3, a redistribution of uniform fishing effort into a reserve allocation decreases production **more** than the same redistribution of any other effort allocation along the same isoquant.

Proof: By Lemma 1, uniform effort maximizes production for that total amount of effort. Because production is strictly decreasing in effort within region 3, a non-uniform level of effort that lies on the same isoquant must be a lower level of total effort. Thus, the corresponding iso-effort intersects the axes closer to the origin, i.e. at a higher level of production. Q.E.D.

The implication of proposition 3 on the surface is essentially the same as that of proposition 1. However, on a deeper level, there is a key difference. In region 3, the fishery is heavily exploited. If a reserve seems more costly than it in fact will be, then analysts would be less likely to recommend one. Yet, in this region, the system is closer to being overexploited. So, choosing not to implement a reserve for allocations in region 3 could be more costly if there were an environmental shock to the system. Whereas, in region 1 choosing not to put in a reserve is likely the best policy anyway.

Proposition 4

For a given isoquant in region 4, a redistribution of uniform fishing effort into a reserve allocation decreases production **less** (or increases production more) than the same redistribution of any other effort allocation along the same isoquant.

Proof: By Lemma 2, uniform effort minimizes production. So, any other point on the isoquant is on a higher iso-effort line, which intersects the axes further from the origin. Points further from the origin correspond to lower levels of production. Q.E.D.

The implication is that in a very heavily exploited fishery, falsely assuming that uniform effort produced the observed harvest gives rise to an overly optimistic evaluation of reserves.

To summarize the implications of Propositions 1-4, consider regions 1-4 as qualitatively representing regions of low, moderate, high, and extreme exploitation. Consider a management model that is calibrated to total fishing catch in the system. Then a naïve assumption that fishing effort is distributed uniformly over space has different implications at different levels of exploitation. At low levels, a marine reserve seems more costly than it really is, but there is little practical significance of this finding. The reason is that managers would be unlikely to consider a reserve in a lightly exploited system. At moderate levels of exploitation, a reserve seems less costly than it really is. If managers are

extremely risk averse, falsely assuming a uniform effort distribution could lead to support for reserves when they are very costly in terms of total harvest. For high exploitation, the bias of assuming uniform effort goes against implementing a reserve. Finally, for extreme exploitation, the bias of assuming uniform effort favors implementing reserves. The point, then, is that the typical effort distribution assumption embedded in most biological models of reserve formation, namely that effort is distributed uniformly, can bias the predicted impacts of marine reserve formation in significant ways and in a manner that depends upon the region in which the status quo is presumed to be located.

V. Simulation with a Beverton-Holt Model and Larval Dispersal

The derivation of the production surface in Figure 4 is based on the standard Beverton-Holt recruitment, which has compensatory mechanisms built into the model structure.⁹ It is also possible that larval dispersal may affect the shape of the steady state production surface. Derivation of a surface comparable to Figure 4 is far more complicated with dispersal, but it is possible to explore the predictions of the previous section with simulations of the steady state.¹⁰ We use parameter values from Wilen et al. (2002) for an eleven-patch metapopulation of red sea urchins, and for simplicity we assume uniform larval dispersal. This is equivalent to a common larval pool in which the number of incoming larvae for each patch in a given year is simply one eleventh of the total larvae produced in the system.

For a fixed amount of fishing effort, we use the Beverton-Holt recruitment parameter a to characterize different levels of exploitation. When a is high, relative exploitation is low, but when a is low, relative exploitation is high. We first run simulations for three different a parameters for a given total fishing effort that is distributed uniformly across the patches. Then we re-run the simulations such that effort in half of the patches is twice the level of effort in the other half of the patches but the total effort in the system is the same. The results of these simple simulations are completely consistent with the analysis above. For $a=0.1$ (a high level), the uniform distribution of effort leads to a higher steady state harvest level than heterogeneous

⁹ It is also possible to introduce depensation directly into the recruitment function and generate another source of non-convexity. See Liermann and Hilborn (2001) for details.

¹⁰ Efforts to derive an explicit analytical expression for a surface with the model in Appendix A have not been successful. To date, we have found only a set of implicit functions that describe the surface.

effort (484,512 kg compared to 464,525 kg). For $\alpha=0.005$ (a low level), the uniform distribution leads to a lower steady state harvest level than heterogeneous effort (246,804 kg compared to 269,963 kg). For $\alpha=0.01$ (an intermediate level), the steady state harvest levels are very close (371,494 kg and 372,067 kg). At a low α , the system is exploited in the extreme region and uniform effort minimizes production. At high α , the system is in the high exploitation region and uniform effort maximizes production. The intermediate α falls near the inflection plane.

V. Discussion

Unlike previous economic analyses of marine reserves, this paper does not address the intertemporal tradeoffs in reserve formation nor does it address the implications of open access in the remaining fishing areas. Instead, it interjects skepticism about a key central claim in the biological literature on reserves: that marine reserves will both generate conservation benefits and increase fishing yields. The claim of increased fishing yields is far less justified when relaxing an obviously inaccurate behavioral assumption. While much of the biological modeling ignores the short-run losses from implementing marine protected areas, even the steady state comparisons are questionable given the biases that result from assuming uniformly distributed behavior.

Ironically, many models of reserves incorporate compensatory mechanisms that ultimately induce biases in analyses that ignore spatial behavior, yet several qualitative arguments for reserves have focused on compensatory mechanisms such as Allee effects. These mechanisms also generate non-convexities in steady state production surfaces but in different ways and may also lead to multiple equilibria. As modelers explore the effects of marine reserves when there is biological depensation, it is important to consider the potential biases that may result with simplifying behavioral assumptions.

A second irony is the role that spatial structure plays in motivating management with marine reserves. In particular, appeals to metapopulation ecology suggest that spatial heterogeneity of the resource and the dynamics of dispersal favor some areas for exploitation and others as breeding

populations to feed exploited areas. Yet, it is inattention to spatial structure in the harvest sector that generates biases in biological models of marine reserves.

The analysis in this work should not be taken as an indictment of marine reserves in general or even specifically as a fishery management tool. Rather, it casts doubt on the existing biological modeling that simplistically depicts fishing behavior as uniformly distributed in space. To make any reliable predictions about the performance of spatial management options therefore requires serious empirical analysis of harvester spatial behavior.

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Appendix A – Derivation of the Beverton-Holt Steady State Production Surface

The following model is based on Botsford et al. (1999) and is the NOECON model that appears in Wilen et al.(2002). Consider a metapopulation with larval dispersal and sedentary adults. Adult organisms grow according to the following von Bertalanffy relationship:

$$Size_{j,a} = L_{\infty}^j (1 - e^{-k_j a}), \quad (A1)$$

where j indexes locations (patches), L_{∞}^j is patch-specific terminal size, a is age, and k_j is a patch-specific growth parameter. $A_{j,a}$ is the number of adults in each patch of each age class. All adult organisms are subject to patch-specific natural mortality (m_j), and ones above the size limit (L_{limit}) are subject to fishing mortality (f_j)

$$A_{j,a} = \begin{cases} A_{j,a} e^{-m_j} & \text{if } Size_{j,a} < L_{limit} \\ A_{j,a} e^{-m_j - f_j} & \text{if } Size_{j,a} > L_{limit} \end{cases} \quad (A2)$$

Catch (C) is a matter of adding up fishing mortality across all locations and age classes weighted by organism size and allometric parameters (w and b) that convert size into biomass.

$$C = \sum_{j=1}^J \sum_{a=0}^{\infty} (1 - e^{-f_j}) w Size_{j,a}^b A_{j,a}, \quad (A3)$$

The following equation describes egg production (e_j) in the system.

$$e_j = \sum_{a=0}^{\infty} \alpha x^{\beta} A_{j,a} \quad \text{where } x = \begin{cases} Size_{j,a} & \text{if } Size_{j,a} > L_{maturity} \\ 0 & \text{if } Size_{j,a} < L_{maturity} \end{cases} \quad (A4)$$

where α and β are parameters that relate organism size to fecundity. Eggs disperse to other locations according to the following:

$$\mathbf{s}^{in} = p \mathbf{D} \mathbf{e} \quad (A5)$$

where \mathbf{s}^{in} is a vector of number of juveniles entering patches, p is survival probability, \mathbf{D} is a dispersal matrix.

Finally, we have the Beverton-Holt recruitment function with parameters a and c :

$$s_j^{out} = \frac{s_j^{in}}{a^{-1} + c^{-1} s_j^{in}} \quad (A6)$$

where s^{out} is the number of juveniles settling out in a location and becoming age zero adults

Consider a two-patch version of the (A.1)-(A.6) in which all larvae disperse to the own-patch, so that the patches are only linked through harvest and not through biology. The metapopulation model essentially has Beverton-Holt models within each patch. We assume that fishing gear has knife-edge selectivity. This means that organisms below the size limit are never harvested but all urchins above the size limit are subject to exploitation. Clark (1990) explains how to obtain steady state yield from a Beverton-Holt fishery with constant recruitment. The basic idea is that integrating over all age classes in the steady state is the same as integrating over the life phases of an individual organism. Continuing to index patch by j , denoting recruits as R , and patch-specific steady state harvest (yield) as y , we have:

$$y_j = R_j f_j e^{\int_{t_\mu}^{\infty} f_j} \int_{t_\mu}^{\infty} e^{-(m+f_j)t} w(t) dt, \quad (\text{A7})$$

where $w(t)$ is the weighting function and t_μ is the age at which an organism is first subjected to fishing mortality. From (A1) and (A2),

$$t_\mu = -k^{-1} \ln \left(1 - \frac{L_{\text{limit}}}{L_\infty} \right). \quad (\text{A8})$$

From (A1) and (A3),

$$w(t) = w \left[L_\infty \left(1 - e^{-kt} \right) \right]^b. \quad (\text{A9})$$

In principle, biological and oceanographic parameters in the model could be patch-specific, but we set them equal to simplify matters and explore questions about effort distribution. Clearly, the integral in (A9) will be problematic without the parameter b taking on an integer value. Typically, this parameter is assumed to be 3.0. See Clark (1990) for an example.

Finding steady state recruits involves finding steady state egg production. We note first that new recruits are simply settlers out, so:

$$R_j \equiv s_j^{out}. \quad (A10)$$

In (A6), we have an expression for settlers out as a function of settlers in. With own-patch dispersal, settlers in is simply a fraction of egg production in the patch, which we can assume for simplicity is one. Using the same logic as in (A7) and substituting for settlers out, the following relationship must hold in the steady state:

$$e_j^{ss} = \left[\frac{e_j^{ss}}{a^{-1} + c^{-1} e_j^{ss}} \right] * \left\{ \int_{t_{mature}}^{t_\mu} [L_\infty (1 - e^{-kt})]^\beta e^{-mt} dt + \int_{t_\mu}^{\infty} [L_\infty (1 - e^{-kt})]^\beta e^{-(m+f_j)t} dt \right\}, \quad (A11)$$

where

$$t_{mature} = -k^{-1} \ln \left(1 - \frac{L_{mature}}{L_\infty} \right). \quad (A12)$$

To continue with analytical expressions, suppose that $\beta=2$. We can then find an implicit expression for steady state egg production as a function of effort and parameters:

$$e_j^{ss} - \left[\frac{e_j^{ss}}{a^{-1} + c^{-1} e_j^{ss}} \right] * \alpha \psi = 0, \quad (A13)$$

where

$$\psi = (L_\infty)^2 \left\{ m^{-1} (e^{-t_{mature}} - e^{-t_\mu}) + (m+k)^{-1} (2e^{-(m+k)t_\mu} - 2e^{-(m+k)t_{mature}}) + (m+2k)^{-1} (e^{-(m+2k)t_{mature}} - e^{-(m+2k)t_\mu}) + (m+f_j)^{-1} e^{-(m+f_j)t_\mu} - 2(m+f_j+k)^{-1} e^{-(m+f_j+k)t_\mu} + (m+f_j+2k)^{-1} e^{-(m+f_j+2k)t_\mu} \right\}. \quad (A14)$$

Thus we have an analytical expression for R_j at different values of fishing mortality. Substituting the result into (A7) and assuming $b = 3$, we can find an analytical expression for steady state yield in each patch:

$$y_j = w R_j f_j (L_\infty)^3 e^{-mt_\mu} \Gamma, \quad (A15)$$

where

$$\Gamma = (m + f_j)^{-1} - 3(m + f_j + k)^{-1} e^{-kt_\mu} + 3(m + f_j + 2k)^{-1} e^{-2kt_\mu} + (m + f_j + 3k)^{-1} e^{-3kt_\mu}.$$

(A16)

In the two-patch system, total steady state yield is simply the sum of patch-specific yields. So, we can depict the production surface in three dimensions. Throughout this section, we refer to the fishing mortality parameter f and fishing effort to be synonymous. In reality, the parameter is a scaled fishing effort.¹¹

¹¹ The scaling of the recruitment parameter is different than in later simulation modeling because we permit infinite horizon organism life cycles and we are abstracting into a two-patch world. Total harvest is also re-scaled to avoid labels that are in scientific notation.

Figure 1

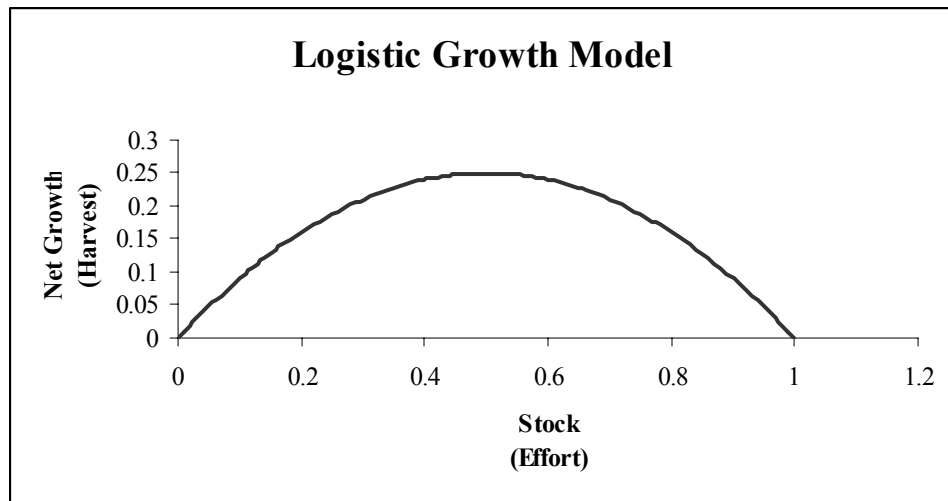


Figure 2

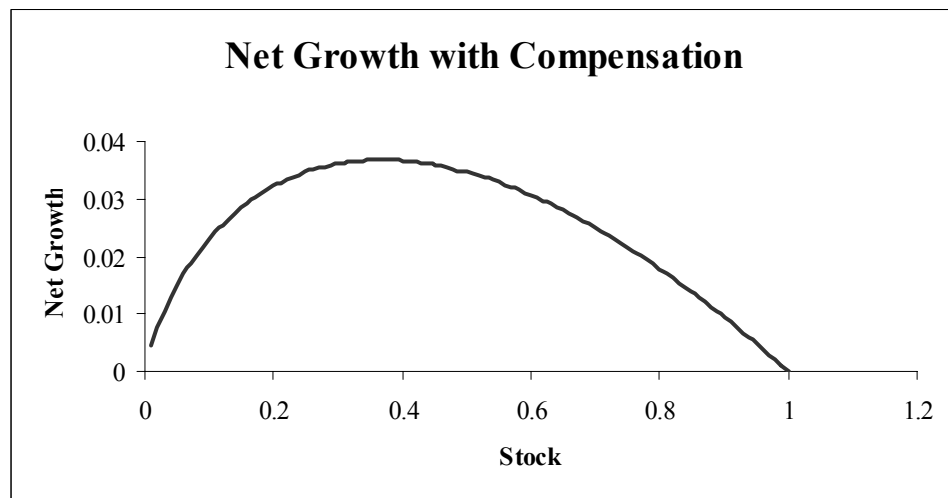


Figure 3

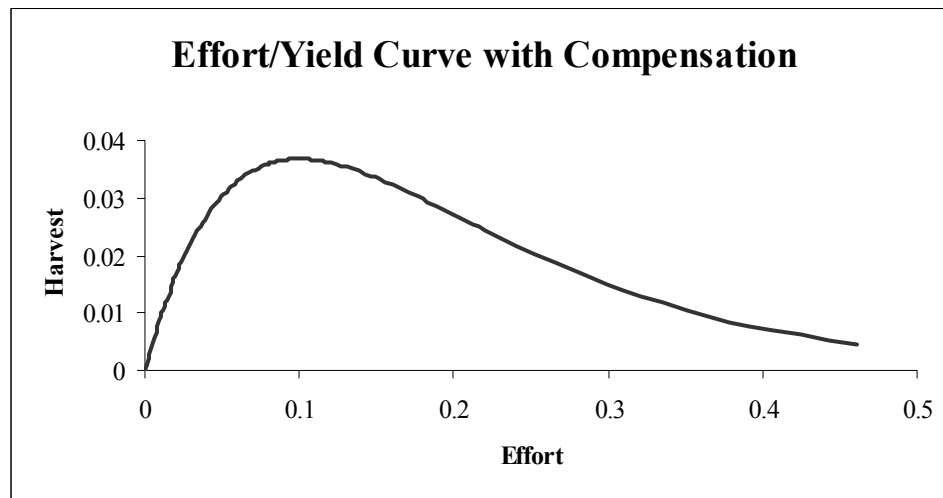


Figure 4

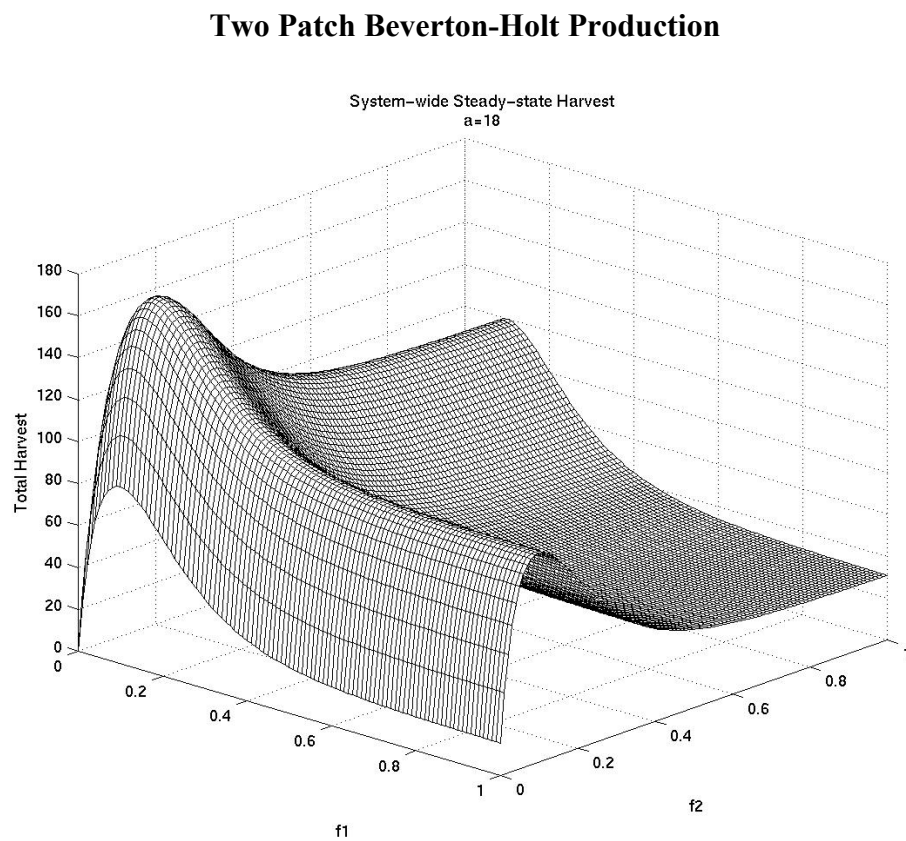


Figure 5
Two Patch Beverton-Holt Production

System-wide Steady-state Harvest
 $a=40$

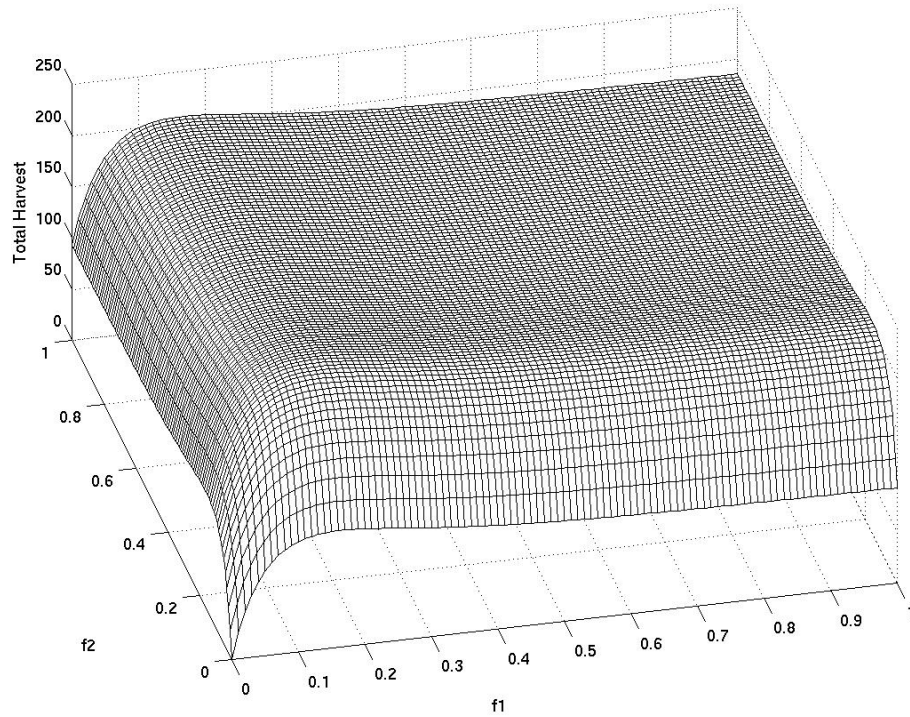


Figure 6
Level Curves for Steady State Production

Total Harvest Level Sets
 $a=18$

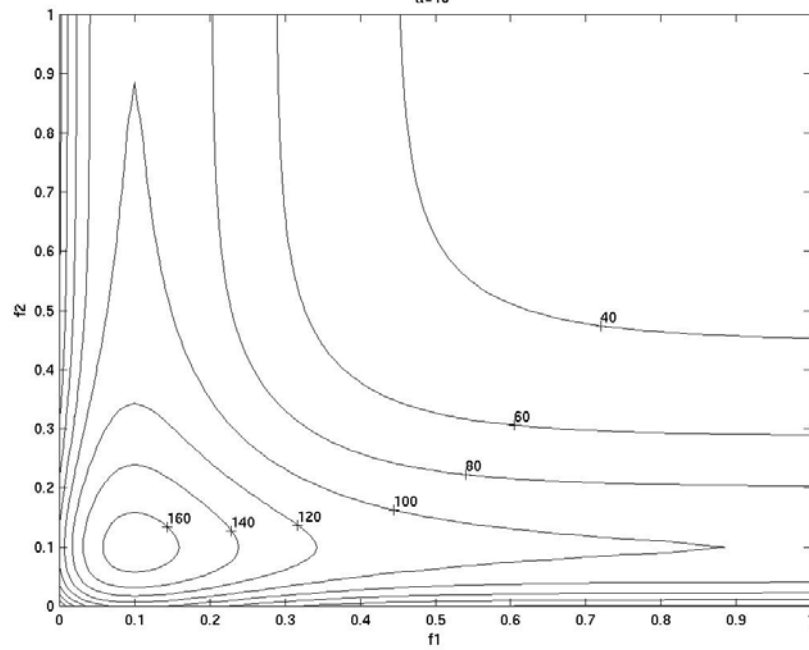


Figure 7
Level Curves for Steady State Production

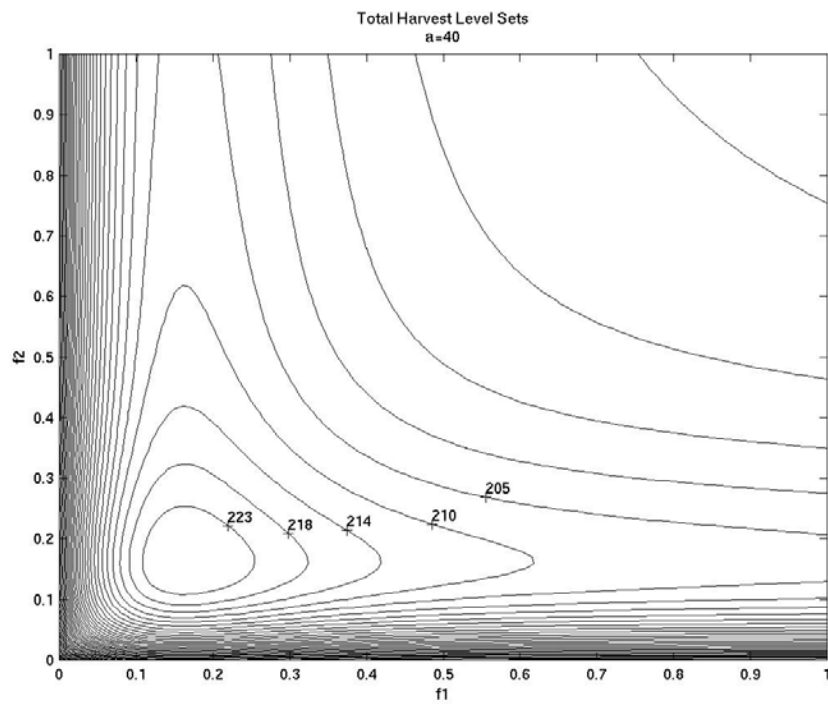


Figure 8
Region Definitions

