Ecological Applications, 00(0), 0000, pp. 000–000
© 0000 by the Ecological Society of America

WHEN ARE NO-TAKE ZONES AN ECONOMICALLY OPTIMAL FISHERY MANAGEMENT STRATEGY?

James N. Sanchirico,[1,5] Urmila Malvadkar,[2] Alan Hastings,[3] and James E. Wilen[4]

[1]*Resources for the Future, 1616 P Street N.W., Washington, D.C., 20036 USA*
[2]*Department of Mathematics, St. Olaf College, Northfield, Minnesota 55057 USA*
[3]*Department of Environmental Science and Policy, University of California, Davis, California 95616 USA*
[4]*Department of Agricultural and Resource Economics, University of California, Davis, California 95616 USA*

Abstract. Discussions on the use of marine reserves (no-take zones) and, more generally, spatial management of fisheries are, for the most part, devoid of analyses that consider the ecological and economic effects simultaneously. To fill this gap, we develop a two-patch ecological-economic model to investigate the effects of spatial management on fishery profits. Because the fishery effects of spatial management depend critically on the nature of the ecological connectivity, our model includes both juvenile and adult movement, with density dependence in settlement differentiating the two types of dispersal. Rather than imposing a reserve on our system and measuring its effect on profits, we ask: "When does setting catch levels to maximize system-wide profits *imply* that a reserve should be created?" Closing areas to fishing is an economically optimal solution when the value derived from spillover from the reserve outweighs the value of fishing in the patch. The condition, while simple to state in summary form, is complex to interpret because it depends on the settlement success of the dispersing organisms, the nature of the costs of the fishing, the economic and ecological heterogeneity of the system, the discount rate, and growth characteristics of the fish population. The condition is more likely to be satisfied when the closed area is a net exporter of biomass and has higher costs of fishing and for fish populations with density-independent settlement ("adult movement") than with density-dependent settlement ("larval dispersal"). Rather surprisingly, there are circumstances whereby closing low biological productivity areas, and even sometimes low cost areas to fish, can result in greater fishing profits than when both areas are open to fishing.

Key words: bioeconomic; fish movement; fishery management; marine reserve; optimal harvest; spatial dynamics; spatial management.

Introduction

Notable declines in marine resource stocks, along with a growing marine conservation movement, have prompted debate over how to manage ocean ecosystems sustainably. Many marine conservationists and scientists are calling for increasing the scale and scope of fishery closures or no-take marine reserves. Some of the potential benefits include conservation of biodiversity, protecting sources of larvae and biomass, increased levels of biomass, increased catches, and providing a hedge against management failures (Carr and Reed 1993, Allison et al. 1998, National Research Council 2001, Botsford et al. 2003, Gerber et al. 2003). To date, the strongest empirical evidence exists for the effects within the reserves, such as increased levels of fish populations, larger individuals, and improvements in species richness (Halpern 2003).

Commercial and recreational fishermen, on the other hand, fear the immediate effects on their livelihoods and the lost access to particular fishing grounds in the future. As the recent deliberations around siting marine reserves off of California (Channel Islands) and Florida (Tortugas) illustrate, these concerns generate passionate political resistance, suggesting future compromises over the location, size, and number of marine reserves are inevitable (Bernstein et al. 2004). Developing models that illuminate the economic and ecological trade-offs involved in siting marine reserves is, therefore, an important task that might reduce conflict over contentious sites, avoid some transaction costs, and avoid disenfranchising various groups in the negotiation process.

The theoretical bioeconomic research on the fishery management effects of marine reserves has focused on measuring their effects compared to the baseline of open access (e.g., Beverton and Holt 1957, Hannesson 1998, Pezzy et al. 2000, Sanchirico and Wilen 2001, Rodwell et al. 2002, Sanchirico 2005), regulated open access (e.g., Hastings and Botsford 1999, Anderson 2002, Hilborn et al. 2006), or limited-entry conditions (e.g., Holland and Brazee 1996, Sanchirico and Wilen 2002, Sanchirico 2004). Under open-access conditions, a typical analysis of a reserve consists of comparing system-wide catch

Manuscript received 29 August 2005; revised 17 January 2006; accepted 27 January 2006. Corresponding Editor: T. E. Essington.

[5] E-mail: sanchirico@rff.org

and biomass levels before and after the reserve is created. For example, Sanchirico and Wilen (2001) identify circumstances for which dispersal benefits (spillover to open areas) due to adult movements are greater than the opportunity cost of closing the area (lost catch), leading to net aggregate catch increases.

In this paper, we set up a framework for identifying potential scenarios for which the positive ecological benefits within reserves can be obtained at the same time that fisheries profits are actually increased. Our stylized analysis asks important practical questions. Under what biological and economic conditions would closing off areas to fishing lead to greater fishing profits than when all areas are open to fishing? How do density-dependent or density-independent settlement processes affect the likelihood that closures emerge as an economically optimal solution? Gerber et al. (2003) raised similar questions when discussing the efficacy of marine reserves.

To address these questions, we develop a spatially explicit bioeconomic optimal control model of two patches. In this model, the regulator chooses the catch rate in the two patches and we investigate conditions under which a marine reserve (setting the catch to zero in one patch) is an economically optimal solution. Fig. 1 illustrates the spectrum of spatial catch rates that we consider in our analysis. Here, an economically optimal solution is one that maximizes the present discounted value (allowing for future profits to be weighted relative to current profits, see Clark [1990]) from the stream of fishery profits from the entire metapopulation.

This paper contributes to the literature in three important ways. First, we focus on the economic profitability of a fishery, which is the primary issue of relevance to fishermen and fishing communities and the metric that drives resistance and political opposition to reserves. Profits may not be proportionate to catch when landed quality varies across patches or when fishing costs depend on spatial factors, such as local abundance and distance to and from the fishing grounds. And, even though catch levels are a measure of interest to gauging the biological health and sustainability of a system, political disagreements over closures will hinge on the economic and ecological effects on the systems. Analyses investigating the effects of reserves in limited-entry settings also consider the effects of reserves on profits (e.g., Holland and Brazee 1996, Sanchirico and Wilen 2002, Sanchirico 2004).

Our second contribution is to exhaustively characterize the conditions for which setting the catch rate to zero in a particular area is an economically optimal policy. We ask, in particular, under what conditions do system-wide fishery returns increase by moving from point A to point B in Fig. 1? No-take zones in our analysis, therefore, are boundary solutions to the more general problem of finding patch-specific optimal catch rates. When point B maximizes fishery profits, no-take zones are the optimal policy relative to all *other* policies that

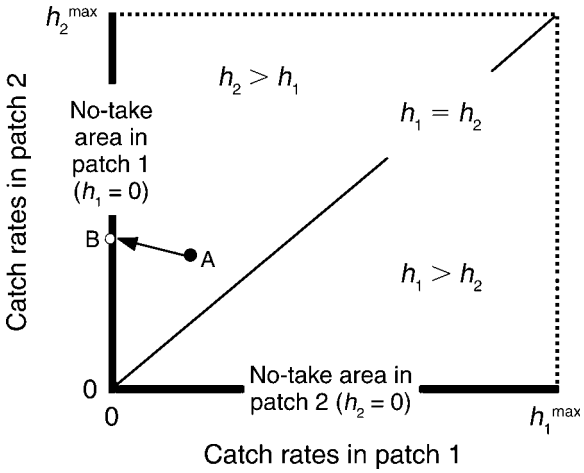

FIG. 1. Management of spatial catch rates with no-take areas as boundary solutions. Our analysis considers all possible catch rates (h_i for $i = 1, 2$) including the cases where the catch rates are set equal to each other and when one or both of the catch rates are set to zero. The latter case identifies when no-take zones are a part of the economically optimal spatial management regime (and are a boundary solution). We ask what parametric and structural circumstances put us at points like B instead of points like A.

regulate catch totals. As such, our analysis is more general than the previous literature.

Our third contribution is that we allow for spatial heterogeneity in both economic and ecological parameters. Economic conditions are likely to differ across space due to factors such as closeness to port and/or bottom conditions (rocky nearshore bottoms vs. offshore sandy shoals). Ecological conditions including growth and mortality and dispersal rates and directions are also likely to differ across space in a patchy system. Under various assumptions incorporating spatial heterogeneity, we analyze cases where the patches are linked by dispersal that is subject to density-dependent settlement (here thought of as juvenile or larvae) and density-independent (adult) settlement processes.

We highlight the importance and role of ecological connectivity by comparing with the benchmark case of optimal catch rates when the patches are biologically independent (not connected by dispersal). When there is no dispersal between the patches, relative profits and optimal catch rates are a function of the biological and economic conditions associated with each independent patch. Low-cost patches will be more profitable, and likely to be more heavily exploited in an economically optimal policy. Then we introduce different types of connectivity via assumptions on the dispersal parameters, such as directional movement (e.g., Tuck and Possingham 2000, Crowder et al. 2000), random movements based on relative densities, and perfect and imperfect mixing of "juvenile" populations (e.g., Rodwell et al. 2002, Sanchirico 2004). Across these different

systems, we investigate conditions under which the economically optimal fishing policy switches from fishing in both patches (point A in Fig. 1) to closing one of the patches to fishing (point B in Fig. 1).

In a closely related paper, Neubert (2003) investigates the issue of how to manage a spatially continuous dynamic system with dispersal, although he focuses on maximizing system-wide physical yield. He reaches the conclusion that the spatial pattern of catch rates that optimizes system-wide *yield* contains areas that are completely closed, as a necessary condition for optimality. Other related papers by Tuck and Possingham (1994, 2000) assume the reserve is a source, patches are homogenous, and the dispersal process exhibits a pre-dispersal density-dependent process. Although we do not model this specific dispersal mechanism, Tuck and Possingham's (1994, 2000) results are qualitatively nested in ours.

While the ecological and economic trade-offs that emerge in the economically optimal solution are complex and varied, some patterns do emerge from our analysis. In accordance with previous studies, we find circumstances where point B in Fig. 1 is optimal (in the literature this is denoted as a win–win situation). Also in accord with earlier studies, we find that reserves are not always part of an economically optimal solution so that sometimes it is optimal to be at point A (interior solution with positive catch rates in both patches). Reserves are *more likely* to be part of the optimal solution when the patch to be closed has higher fishing costs and/or the patch is a strong net exporter of biomass to the fished area. We also find that populations with density-independent settlement in the dispersal process are more likely to have closures as part of the optimal solution than those with density-dependent settlement larval.

Some surprising and counterintuitive results emerge from our analysis. First, there exist circumstances for which fishing profits are maximized when the patch with the lower cost of fishing is closed. This occurs when the strength of the spillover effect from the reserve is great enough to outweigh the loss in profitability from closing the lower cost patch. Second, closing the low rather than the high biologically productive patch is more likely to lead to an increase in fishery profits. This conclusion runs counter to common advice that closing the high biologically productive areas will directly benefit fishermen. Intuitively, this result stems from the fact that the high biological productive patches are also the ones that contribute a relatively larger share to the system-wide profits.

In addition to finding conditions for which setting the optimal catch rate to zero maximizes profit, our model highlights the biological *and* economic importance of ecological connectivity, density-independent and -dependent settlement mechanisms, and spatial heterogeneity. While more specific models might be more realistic for a particular marine species, our general model illuminates qualitative properties of spatial and dynamic economic-ecological systems—properties that improve our understanding of how to manage more complex systems (Hilborn et al. 2003). As such, our model can be used to investigate other types of spatial management, such as employing different intensities and types of uses in a zonal system.

Ecological Model

Our bioeconomic model treats space explicitly in the form of two discrete patches; fish populations may disperse between the patches via various mechanisms at a variety of rates. Focusing on two discrete patches with connectivity may seem restrictive, but, as in Hastings and Botsford (2003), one can argue that such an approach can approximate models with space treated continuously. In models that treat space homogeneously, the distance between habitats is the only relevant aspect of the location of the habitats in space. In a patchy environment, however, it is easy to imagine that reserve location, and not just relative position, is critical, if the reserve is to be biologically and economically optimal. Our framework is especially suited to investigate how patch or habitat heterogeneity interacts with dispersal and connectivity to affect the potential benefits from closures. Because we allow for population dynamics in both patches, we do not impose the "scorched earth" assumption, namely that all fish that leave the reserve are harvested (see, for example, Hastings and Botsford 1999). Our model, therefore, better mimics actual systems, such as the recent system of reserves established in the Channel Islands or the closed areas on the Grand Banks.

Developing a realistic spatial model of a fish population that is both general and simple enough to make predictions is a difficult endeavor for a couple of reasons. First, for many fish (reef fish for example), the presence and strength of density dependence is uncertain (Sale 1991 and Caley et al. 1996 as cited in Forrester and Steele 2000) and likely to be scale and context dependent (Steele 1997, Forrester and Steele 2000). Second, it is difficult to justify any particular model relating the number of spawners to recruits (e.g., Quinn and Deriso 1999) because recruitment can be so highly variable. Furthermore, the classic models of fisheries (see review in Quinn and Deriso 1999), such as the Beverton-Holt model, have typically been formulated as discrete-time models and therefore cannot be used to look at systems with both "juvenile" dispersal and "adult" movement during the year. Because adults can move into and out of or between patches within a single year, and may or may not be caught in different locations, one needs to use a continuous-time model when accounting for adult movement unless the adult movement only occurs during a specific time frame. Third, the movement of individuals among patches is still a topic about which far too little is known (e.g., Shanks et al. 2003) and

movement rates appear to be highly variable among even closely related species.

One aspect of the movement of fish and invertebrates that is becoming better known is the degree to which individuals are essentially retained in their natal habitat (e.g., Swearer et al. 2002, Thorrold et al. 2002, Warner and Cowen 2002). Although this is still a difficult issue, this partial knowledge of the degree of local retention can be used within the context of heuristic models to understand how connectivity may influence optimal fishery policy. In particular, if we consider a model with just two patches, knowledge of the degree of local retention can be used to begin to get parameter values for the dispersal rates in this kind of model.

Given our current limited knowledge, models and results that derive general qualitative principles are likely to be of the most use, since we simply do not have the data to make more detailed predictions, or to justify the use of particular models. While there are certainly complexities in marine systems that are overly simplified in our model or fall outside its scope, our relatively simple structure is justified by appealing to Occam's razor and starting with the simplest model which still captures fundamental forces.

We begin with two habitats or patches with population densities x_1 and x_2. The populations are assumed to grow at rates $F_1(x_1, x_2)$ and $F_2(x_1, x_2)$, which depend on the population densities in both areas. In particular, the population dynamics within each patch are

$$\begin{aligned}\frac{dx_1}{dt} &= F_1(x_1, x_2) - h_1 \\ &= (A_1x_1 + B_1x_2)(1 - x_1) + d_{12}x_2 - d_{11}x_1 - h_1 \quad (1)\end{aligned}$$

$$\begin{aligned}\frac{dx_2}{dt} &= F_2(x_1, x_2) - h_2 \\ &= (A_2x_2 + B_2x_1)(1 - x_2) + d_{21}x_1 - d_{22}x_2 - h_2 \quad (2)\end{aligned}$$

where h_i is the catch level in patch i.

For a single isolated patch (for example, let $x_2 = 0$ in Eq. 1), the population density x_1 increases logistically with a growth rate A_1 but loses individuals at a density-independent per-capita rate d_{11}. When a second patch is included in the dynamics, we consider two possibilities for fish from the second patch settling into the first patch. First, the settlement rate may be a function of the density in the first patch (which is denoted by the term $B_1x_2(1 - x_1)$). With this formulation, dispersing organisms from patch x_2 will have the largest influence on patch x_1's growth when the population in x_1 is small ($[\partial F_1(x_1, x_2)]/\partial x_2 = b_1(1 - x_1) + d_{12}$). Second, the settlement rate may be independent of the density in the first patch (denoted by the term $d_{12}x_2$). These two mechanisms can be thought of as juvenile and adult settlement, respectively, with adult survivorship assumed unaffected by density dependent mechanisms. This characterization is likely when the species have higher mortality rates due to predation at younger life stages.

While this model is very general, there are some logical restrictions on the dispersal parameters that should be imposed to ensure that what leaves one area is greater than or equal to what arrives in another. (This restriction disallows the possibility of biomass entering the system from patches other than the two we consider.) With respect to adult dispersal, we assume that there is no mortality during dispersal and that what leaves patch i for patch j arrives in patch j. This is equivalent to assuming that $d_{ii} = d_{ji}$.

With respect to juvenile dispersal, we assume that juveniles produced in patch i will either settle in patch i, settle in patch j, or settle in neither patch (e.g., mortality during the settlement process). We allow for the possibility of mortality by imposing the restriction that $A_i + B_j/m_j \leq a_i^0$ where m_j is the probability of juvenile survival during the dispersal process, and a_i^0 is the growth rate produced by patch i when there is no connectivity (all juveniles settle in the local patch with no mortality). When B_2 is equal to zero and all juveniles in patch 1 are retained locally with no mortality, we have $A_i = a_i^0$.

We can rescale the growth rates A_i and B_i to reflect the adding-up constraint, where $a_i = A_i/a_i^0$ and $b_j = B_j/a_i^0$. The new constraint is $a_i + b_j/m_j = 1$, where b_j can now be interpreted as the share of larvae produced in patch i that contributes to population growth in patch j. Unless otherwise noted, we will assume that both m_j are equal to 1 and that the above constraint holds with an equality.

For many species, adults and juveniles are likely to have different rates of movement and dispersal processes, since currents largely transport juveniles, whereas adults may have more directed and purposeful movement. By allowing the d_{ij} and b_j to vary, many possible connectivity structures and dispersal processes may be captured in Eqs. 1 and 2. Assume, for example, that $d_{12} = d_{22} = b_1 = b_2 = 0$ and $d_{21} = d_{11} > 0$. Then patch 1 is a source and patch 2 is a sink with only density-independent settlement (e.g., Holt 1985, Pulliam 1988, Crowder et. al. 2000). We can also model the case where patch 1 is a source and dispersing biomass is subject to density-dependent settlement ($b_1 = 0$, $b_2 > 0$, and $d_{ij} = 0$).

When the dispersal parameters are all positive, the direction and level of dispersal and settlement will depend on the relative densities and dispersal parameters. In the aggregate, we classify patches as net exporters (net sources) or importers (net sinks) of biomass density. With density-independent settlement only, patch 1 is net exporter, for example, if the net dispersal term $d_{12}x_2 - d_{11}x_1$ is positive. We could have, for example, a patch that is a net importer of "juveniles" and a net exporter of "adults." When we link the ecological and economic submodels, the classification of patches as net exporters or importers will also depend on the level of fishing in each patch, since fishing affects the relative densities of fish in the two populations.

While much of the current theory explaining the potential utility of reserves (e.g., Hastings and Botsford

1999, Botsford et al. 2001) considers situations in which adults are stationary and larvae disperse, it is not immediately clear how conclusions carry over to the important case where adults are mobile. An advantage of Eqs. 1 and 2, therefore, is that we nest within a single formulation (albeit ad hoc) various dispersal mechanisms and rates. The model also highlights the importance of the timing of density dependence effects relative to dispersal processes (Forrester and Steele 2000, Gerber et al. 2003).

Without fishing ($h_i = 0$ for $i = 1, 2$), the system will approach an unexploited biological equilibrium. For biological realism, we assume that the parameters are such that a stable, positive equilibrium exists. Formally, a population density (x_1^b, x_2^b) is said to be at its biological equilibrium if $F_1(x_1^b, x_2^b) = F_2(x_1^b, x_2^b) = 0$. It is easy to see that if the patches are disconnected from each other (so-called closed biological system), the biological equilibrium is equal to 1 in each patch (since we have scaled population size to be measured in density). This is also true with only juvenile settlement.

Economic Model

In characterizing an optimal fishery management policy, ecologists often focus on maximum sustainable physical yield. But as Clark (1990) explains, this completely ignores many of the relevant economic considerations. Following Clark (1990), we focus on a fishery for which a regulator has direct and complete control of catch levels and for whom the objective is to maximize the present discounted value of fishery profits (as opposed to maximizing sustainable yield) by choosing the catch levels in each patch $\mathbf{h}(t) = (h_1(t), h_2(t))$.

To solve this problem, we determine catch as a function of time in each patch, assuming that catch is constrained between 0 and $h_{i,\max}$: $0 \leq h_i(t) \leq h_{i,\max}$. If, under some conditions, it is economically optimal from the system-wide perspective to set equilibrium $h_i(t) = 0$ for patch i, then a reserve emerges. Note that, in our formulation, a reserve is not imposed to satisfy some external biological goal, but rather it emerges as a part of the optimal catch strategy for the system (recall point B in Fig. 1). We seek to determine conditions under which having a reserve is an economically superior fishing policy to having some catch in both patches. These circumstances should be less contentious politically, since they avoid pitting advocates for the biodiversity conservation benefits of reserves against user groups who view no-take zones as impinging on livelihoods.

The objective function of the regulator to be maximized is formally written as

$$J(\mathbf{h}) = \int_0^\infty \exp(-\delta t)\left\{\left[p_1 - \frac{c_1}{x_1}\right]h_1(t) + \left[p_2 - \frac{c_2}{x_2}\right]h_2(t)\right\}dt$$

where p_i is the price received at the dock from fish in patch i, c_i is a fishing cost parameter in patch i, and δ is the social discount rate (Clark 1990). We allow prices to vary across space due to differences in product quality, but, for simplicity, assume prices remain constant over time. We also assume that prices for the fish are not responsive to changes in catch levels as, for example, when the fishery in question delivers to a large and global market.

The per-unit costs of catching fish in patch i is c_i/x_i and is a function of two components; the (density) level of the fish population in the patch and a patch-dependent cost parameter. Unit fishing costs are assumed to be stock dependent so that unit costs decline as population density increases. The constants c_i represent factors (unrelated to population size) involved in fishing a particular area, such as distance from fishing grounds (patches) to port. Operating costs could also differ across patches due to oceanographic conditions and sea floor topography. Whether per-unit costs of fishing in period t are low or high in an area depends, therefore, on both the fish stock size and the cost of operating in the area. For example, patches that are farther offshore (greater c_i than inshore areas) may have lower unit costs than inshore patches if offshore population density effects outweigh fundamental cost factor effects.

Similar bioeconomic models have been developed in other settings to address different questions. For example, Tuck and Possingham (1994) investigate optimal management in a two-patch sink–source system with no economic heterogeneity, and Brown and Roughgarden (1997) use an optimal control model with larval dispersal to illustrate the value of larval pools to system-wide fishery profits. Other studies are by Huffaker et al. (1992), Skonhoft and Solstad (1996), Jannmatt (2004), and Sanchirico and Wilen (2005). We assume, as do the aforementioned studies, that the regulator is knowledgeable, understanding population dynamics and dispersal mechanics of the biology, with perfect foresight.

Optimal Spatial Catch Rates and Fish Densities

Because the solution techniques for our type of optimal control problem are well documented in Clark (1990) and Kamien and Schwartz (1991), we present them in an Appendix. The optimal catch in each period is determined from maximizing the objective function subject to the population growth equations (1 and 2) and a set of initial conditions. The Appendix also describes how to calculate the optimal values of the biomass density (or, in an unscaled version, population size) and the catch when the system is at the optimal solution.

As the Appendix shows, the solution to the problem can be expressed as two equations that implicitly define the optimal (steady-state) equilibrium biomass densities (x_1^*, x_2^*), which depend on biological growth and dispersal parameters as well as the economic parameters

$$
\begin{aligned}
&(\delta - a_1 + 2a_1x_1)\left(p_1 - \frac{c_1}{x_1}\right) - \frac{c_1}{x_1^2}a_1x_1(1-x_1) \\
&\quad = -d_{11}\left(p_1 - \frac{c_1}{x_1}\right) + d_{21}\left(p_2 - \frac{c_2}{x_2}\right) + \frac{c_1}{x_1^2}(d_{12}x_2 - d_{11}x_1) \\
&\qquad - b_1x_2\left(p_1 - \frac{c_1}{x_1}\right) + b_2\left(p_2 - \frac{c_2}{x_2}\right)(1-x_2) \\
&\qquad + \frac{c_1}{x_1^2}b_1x_2(1-x_1) \qquad (3)
\end{aligned}
$$

$$
\begin{aligned}
&(\delta - a_2 + 2a_2x_2)\left(p_2 - \frac{c_2}{x_2}\right) - \frac{c_2}{x_2^2}a_2x_2(1-x_2) \\
&\quad = -d_{22}\left(p_2 - \frac{c_2}{x_2}\right) + d_{12}\left(p_1 - \frac{c_1}{x_1}\right) + \frac{c_2}{x_2^2}(d_{21}x_1 - d_{22}x_2) \\
&\qquad - b_2x_1\left(p_2 - \frac{c_2}{x_2}\right) + b_1\left(p_1 - \frac{c_1}{x_1}\right)(1-x_1) \\
&\qquad + \frac{c_2}{x_2^2}b_2x_1(1-x_2). \qquad (4)
\end{aligned}
$$

The terms on the left hand side of Eqs. 3 and 4, which are derived by rearranging Eq. A.5 in the Appendix, are the conditions that define the optimal biomass density levels in a closed ecological system, where all connectivity parameters are zero (b_i and d_{ij}). In a non-spatial system, Clark (1990) has shown that the optimal biomass density level just makes the value of a (instantaneous) reduction in biomass density from catching one more unit of fish today (profit from selling the fish) equal to the present discounted value of the loss from the long term reduction in the steady state biomass density from that additional catch taken today.

When each patch is independent, closed form analytical solutions to Eqs. 3 and 4 are possible and the optimal equilibrium biomass densities are functions only of own-patch specific economic and biological parameters. (See the Appendix for derivation and details). It can be shown that the higher the operating cost, c_i, the higher the optimal biomass density, and the higher the price of fish, the lower the optimal biomass density, all things being equal (Clark 1990). Optimal density levels are also inversely related to the discount rate.

Eqs. 3 and 4 illustrate, however, that there are other benefits and costs that must be considered in a system of ecologically connected patches. For example, in a connected system, removing one unit of steady-state biomass density in patch 1 affects spillover of adults and juveniles into patch 2, as well as density-dependent survival of juveniles migrating into patch 1 from patch 2.

While the optimal biomass density levels will depend on the simultaneous solution of these equations, it is possible to describe patch-specific economic effects to provide intuition about the importance of ecological connectivity at the sustainable solution. Generally speaking, a unit of biomass density that leaves a patch for another could have been caught in its origin. This represents a loss in potential net profits in the patch of origin. However, all is not really lost, because the biomass can be caught at its destination instead. (With mortality in the dispersal process, there is a potential loss.) Whether a unit of biomass density is more "valuable" in terms of profit in one or the other patch depends on the relative prices and costs in the two patches. In addition, movement of biomass across space affects the standing population levels in the patches, and as such, the costs of fishing, which are stock dependent. Density-dependent or -independent settlement will modify the form of these three effects, but the intuition remains the same.

Consider first the economic effects associated with connectivity at the optimal biomass level in the presence of "adult" dispersal (also discussed in Sanchirico and Wilen 2005). If there is no "juvenile" dispersal, only the first three terms on the right hand side of Eq. 3 apply. The first term $-d_{11}(p_1 - (c_1/x_1))$ is the (instantaneous) loss in marginal profits from a one-unit sustained reduction in biomass density in patch 1, where $[p_1 - (c_1/x_1)]$ is the sustainable (per-unit) profit from catching fish in patch 1. A fish that leaves patch 1 and enters patch 2, however, can be caught in patch 2. The second term, $d_{21}[p_2 - (c_2/x_2)]$, measures the sustained returns from catching the fish that migrates from patch 1 into patch 2. The (marginal) change in biomass density in patch 1 (holding biomass in patch 2 constant) due to dispersal will also affect the costs of fishing, because of the assumption that fishing costs depend on the density of the standing fish stock. The third term reflects this cost effect, $(c_1/x_1^2)(d_{12}x_2 - d_{11}x_1)$, where the second component is the net dispersal in patch 1. Positive net dispersal implies fish are, on net, entering patch 1 (patch 1 is a net importer). The cost effect is the change in the total cost of fishing in patch 1 that results from an infinitesimal increase in fish in patch 1.

How does density dependent settlement affect the optimal spatial catch rates? This can be addressed by examining Eq. 3, suppressing "adult" dispersal by assuming that the d_{ij} are equal to zero. The first term $b_1x_2[p_1 - (c_1/x_1)]$ is the (marginal) loss in sustainable profit in patch 1 due to the competition between juveniles arriving from patch 2 and those already present in patch 1.

The second term, $b_2[p_2 - (c_2/x_2)](1 - x_2)$, represents the change in net sustained profits in patch 2 associated with juveniles that leave patch 1 and are caught in patch 2. Everything else being equal and this term being smaller, the greater the density of fish in patch 2, reflecting the density dependent survival there. Because juveniles that arrive in a patch are instantaneously subject to the growth process in the patch, the growth/settlement rate scales this effect. Although immigrant juveniles from patch 2 lower the potential investment returns in patch 1 via their effect on the biological growth process (a reduction of the growth rate), they also affect the standing population density in the patch. With stock dependent costs, higher population densities imply lower costs.

The third term, $(c_1/x_1^2)[b_1x_2(1 - x_1)]\ (c_1/x_1^2)$, represents the change in patch 1′s sustained fishing costs due to the

shuffling of biomass (juveniles) density across the patches. The term out front is the change in the unit cost of fishing in patch 1. The term in brackets is the share of sustainable catch in patch 1 due to the influx of juveniles from patch 2. This can be seen by noting that the steady-state catch in patch 1 is equal to $h_1 = a_1x_1(1 - x_1) + b_1x_2(1 - x_1)$. Therefore, the term reflects the change in total (sustainable) costs of catching fish in patch 1 that is attributable to the juveniles arriving from patch 2. Unlike the density-independent settlement case, the magnitude of this effect depends directly on the density of the resident fish population.

With both adult and juvenile settlement occurring, the regulator needs to tradeoff not just economic values associated with standing biomass in the local patch, but also the value associated with "nature's" reallocation via various dispersal processes. Because the regulator is setting the optimal catch in each patch, she will need to tradeoff catching more fish in patch 1, which implies lower population levels and therefore fewer adults and juveniles dispersing to patch 2, against catching fewer fish in patch 1 and shifting effort to patch 2. This tradeoff explicitly accounts for the relative profitability associated with harvesting in each patch, itself a function of bioeconomic parameters associated with each patch as well as with the nature of connectivity between patches.

When Are No-Take Zones an Economically Optimal Fishery Management Strategy?

We now turn to the question: under what economic and biological conditions are reserves, or permanent fishery closures, a feature of an economically optimal management plan? In other words, when is completely closing a patch (point B in Fig. 1) superior to having non-zero fishing levels in both patches (point A in Fig. 1)? We are interested in how the different types of dispersal processes and strengths increase or decrease the feasible region over which reserves are optimal relative to the case with no connectivity. For example, are reserves more likely to be part of the economically optimal solution in systems with density independent settlement than in systems with density dependent settlement?

In this system, a reserve is the optimal long-term management strategy whenever the optimal catch level is a boundary solution with $h_i = 0$ at the steady state. In what follows, we analyze separately which specific ranges of fishing cost c_i and biological growth a_i parameters lead to a boundary solution. We choose to highlight the role of costs because, while most of the natural science articles on marine reserves focus on yields (e.g., Hastings and Botsford 1999, Tuck and Possingham 2000, Nuebert 2003), differential costs are important determinants of site selection under economic objectives (e.g., National Research Council 2001, Sanchirico and Wilen 2001, Sanchirico 2004). Investigating growth rates sheds light on whether highly (biological) productive patches are more likely to lead to optimal fishery closures than lower productivity patches.

In each case, we rely on numerical solutions to provide insight into these questions. Without loss of generality, we focus on the costs and intrinsic growth rates in patch 1, which is our reserve designate patch, and patch 2 is the patch to be left open to fishing. Let Ψ be the parameter of interest in patch 1 (c_1 or a_1). We seek the critical value of Ψ, denoted Ψ^{crit}, which is the level of Ψ that generates $h_1 = 0$, i.e., closure as an optimal solution, given a set of biological and economic parameters.

We solve for the set (Ψ^{crit}, x_1^*, x_2^*) by simultaneously solving Eqs. 3 and 4, and $F_1(x_1, x_2) = 0$. The resulting solution, therefore, satisfies the conditions for economic optimality and that the catch rate in patch 1 is 0 or $h_1 = 0$. The catch in patch 2 is then determined at its equilibrium value by $F_2(x_1^*, x_2^*) = h_2^*$. We solve for ($\Psi^{\text{crit}}$, x_1^*, x_2^*) by varying the dispersal rates to understand how dispersal and the types of settlement affect the likelihood of a reserve being part of the optimal solution.

In the simulations, unless otherwise stated, we assume that all parameters are the same across the patches. Prices are equal to 1 and a discount rate of 7% is used. We also perform sensitivity analysis on the discount rate and on the assumptions regarding parameter homogeneity.

Operating cost of fishing

We first examine how costs of fishing affect the possibility that a reserve is part of an economically optimal solution. Specifically, we solve for the triplet (c_1^{crit}, x_1^*, x_2^*) where the critical value of cost is denoted c_1^{crit} and denotes the level of c_1 that generates $h_1 = 0$, i.e., closure as an optimal solution, given a set of biological parameters and cost in the second patch ($c_2 = 0.25$). For any level of costs greater than or equal to c_1^{crit}, patch 1 is optimally closed to fishing and for any levels below c_1^{crit}, the optimal catch rates in both patches are non-zero.

With certain sufficiently simple systems, we can solve for the critical values analytically. For example, assume that the ecological system is spatially independent or closed. Then a reserve in patch 1 implies that the optimal population must be at the natural equilibrium of 1. Given that the unit price of harvest is 1, the critical cost coefficient in patch 1 that generates this is also equal to 1 ($c_1^{\text{crit}} = 1$). As we mentioned previously, this case represents an important benchmark where the optimal catch rates depend only on the patch specific parameters. With $c_1 \geq 1$ and $c_2 < 1$, the optimal solution is to have no fishing in patch 1. It is important to note that the motivation for no fishing in patch 1 is not because of the potential spillover effects, as there are none in this case, but rather because it is simply not profitable to fish in patch 1 with such high costs. We can also show analytically that when patch 1 is a sink patch $d_{12} > 0$, $d_{21} = d_{11} = 0$, and $b_2 = 0$, closing patch 1 is optimal under the same conditions as when the system is closed. Tuck and Possingham (2000) find a similar result.

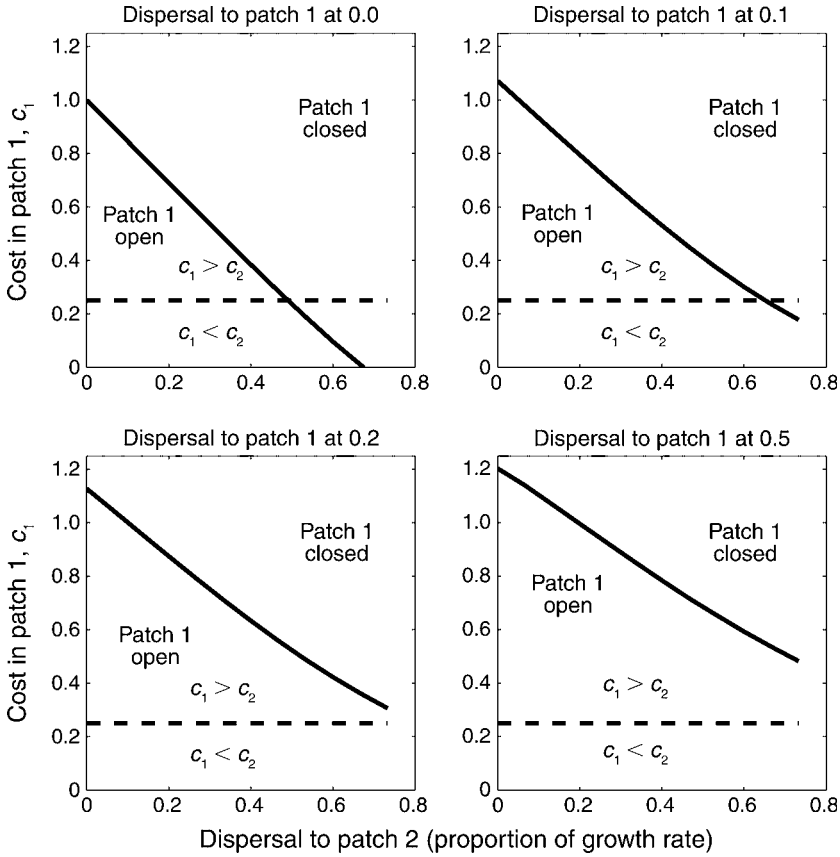

FIG. 2. Density-independent settlement and critical cost coefficient levels for different dispersal rates to patch 1. By holding dispersal to patch 1 (reserve designate in our analysis) fixed at a particular level, we illustrate how the critical cost coefficient changes as the dispersal from patch 1 (reserve designate) to patch 2 (fished area) increases. Regions in the panels illustrate solutions for which it is optimal to have both patches open to fishing ($c_1 < c_1^{\text{crit}}$) or to close patch 1 to fishing ($c_1 \geq c_1^{\text{crit}}$). The dashed line represents the cost coefficient assumed for patch 2 (c_2) and the solid line represents the critical cost level (c_1^{crit}). When the critical cost level is below the dashed line, it is optimal to close the low-cost patch. The upper left panel represents the case of unidirectional dispersal (patch 1 is a source and patch 2 is a sink). The other panels represent different dispersal regimes with respect to the dispersal flowing from patch 2 to patch 1.

In an ecologically connected system, we can examine how various dispersal rates in each patch affect the critical cost parameter. For example, we ask, would it ever be optimal to shut a patch down with connectivity, when the cost coefficient in that patch is below 1? By varying the dispersal rates in each patch, we can map out how the critical cost coefficient changes under different conditions. While we allow that the movement rates d_{ij} can differ from one patch to the other, we will assume conditions that imply no loss during settlement. That is, the flow of fish leaving one patch is assumed the same as the flow entering the other patch. To focus on the effects of "adult" dispersal, the "juvenile" connectivity parameters b_i are first set to zero.

Before illustrating the general case where we vary "adult" dispersal both to and from patch 1, we present the levels of c_1^{crit} as a function of the dispersal rates d_{ij} from patch 1 to patch 2 (here measured as a proportion of the intrinsic growth rate in the patch). We do this by holding the dispersal rate from patch 2 to patch 1 constant. Fig. 1 illustrates the relationships for four levels of dispersal rates from patch 2 to patch 1 measured as a proportion of a_2 including (0, 0.1, 0.2, 0.5).

The northwest panel in Fig. 1 illustrates the case where dispersal is unidirectional from patch 1 to patch 2 (dispersal from 2 to 1 is zero). In other words, patch 1 is a pure source and patch 2 is a sink. While not a likely situation in the marine environment, this case bounds the potential solutions and provides intuition for the more complex scenarios. For cost levels less than the critical cost, both patches are optimally open to fishing and for levels above or equal to the critical cost coefficient, closing patch 1 to fishing is part of the optimal solution. The origin represents the closed biological system (dispersal to either patch is zero), where $c_1^{\text{crit}} = 1$. We also show (for reference) the cost level in patch 2 (c_2).

Overall, we find that the critical cost coefficient decreases as the dispersal from patch 1 to 2 increases. For low dispersal levels, $c_1^{\text{crit}} > c_2$, implying that for a no-take zone to be optimal, the cost differential between

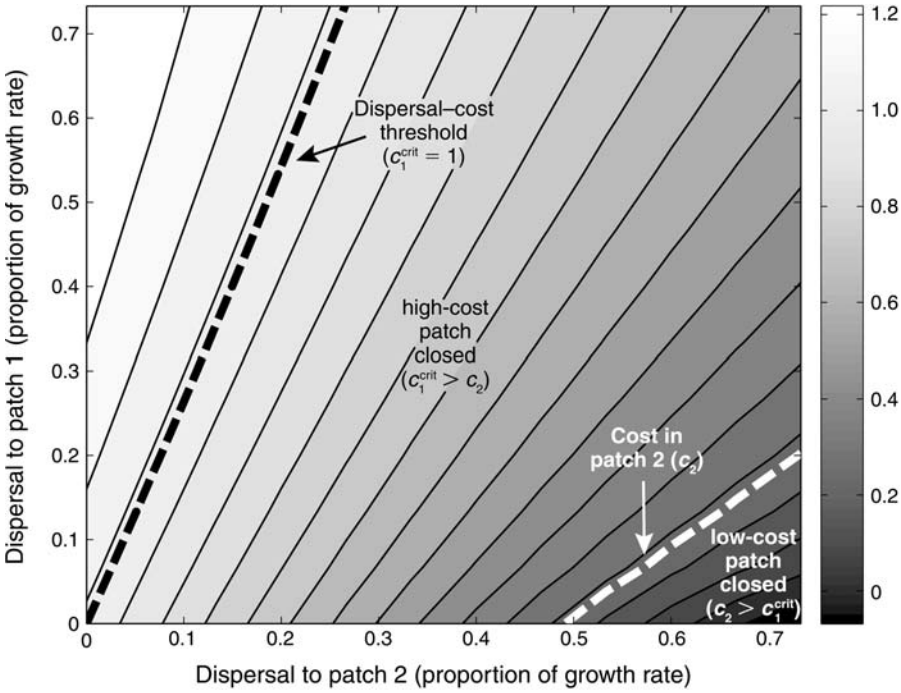

FIG. 3. Density-independent settlement and critical cost coefficient levels. The dispersal rate is measured as a proportion of the patch intrinsic growth rates. The y-axis corresponds to the case where patch 1 is a sink, and the x-axis corresponds to the case where patch 2 is a source. The contour lines correspond to critical cost levels for which closing patch 1 to fishing is part of the optimal solution. To the left of the "dispersal cost threshold" line, critical cost coefficient levels are greater than 1 and, to the right, the critical coefficients are less than 1. The area to the right of the threshold illustrates conditions where patch 1 would be too high cost to operate in if there were no spillover coming from patch 2 to reduce the cost of fishing. To the right of the line identifying the assumed fishing cost coefficient in patch 2 is the area where the critical cost coefficients for closing patch 1 fall below the cost coefficient in the patch open to fishing. The region between the two dashed lines represents the area where the critical cost coefficient is less than 1 (so fishing would occur if the patches were not biologically connected), but for which (due to dispersal) the optimal solution consists of closing the patch to fishing.

the patches must be considerable (e.g., due to travel costs). As the dispersal levels from patch 1 to patch 2 increase, c_1^{crit} decreases and eventually we find that no-take zones are optimal even when there is no heterogeneity in the parameters of the system ($c_1^{crit} = c_2$ and growth rates are identical). For high dispersal levels, it is even possible that closing the low cost patch is optimal, where $c_1^{crit} < c_2$. This is a counterintuitive case whereby it is economically efficient to close the patch with the lower operating cost. This occurs because sufficiently high dispersal rates cause the spillover benefits from the closing the patch to outweigh the (also relatively high) lost profitability of closing the patch. Previous studies that focus on source–sink systems with no patch heterogeneity have discussed the case where $c_1^{crit} = c_2$.

The other three panels represent different dispersal rates to patch 1 from patch 2. As this rate increases, the potential net spillover benefits from closing patch 1 decrease. Because the spillover benefits decrease, the critical cost coefficient level such that it is optimal to close patch 1 increases. The implication is that, for an optimal no-take zone, the cost from closing the patch (lost profitability) must be low and this occurs with higher cost coefficients, everything else being equal. This can be seen by holding the dispersal to patch 2 fixed at a level and comparing the critical cost parameter across the panels in Fig. 2. As the two lower panels in Fig. 2 illustrate, with low net spillover benefits, it is never the case that it is optimal to close the low-cost patch ($c_1^{crit} > c_2$). It is important to note that this holds even for high dispersal rates to patch 2. The reason is that what matters for an optimal no-take zone is not the absolute dispersal rate but the relative rates when dispersal is presumed to flow in both directions.

We use a contour plot, Fig. 3, to illustrate the general solution where both dispersal rates are varied. The case with no dispersal is at the point (0, 0). The panels in Fig. 2 are nested within this surface. Holding dispersal into patch 2 at zero (moving along the y-axis in Fig. 3), the critical cost parameter increases as the dispersal rate into patch 1 increases. As discussed earlier, when the dispersal rate increases and there is a net flow into the patch, the (marginal) cost of fishing will be lower. The increase in the "standing stock" of biomass reduces the costs of fishing (makes the patch more profitable to operate in), which implies that, for patch 1 to be closed optimally, the unit operating cost of fishing must increase to justify closing the patch. The corollary is

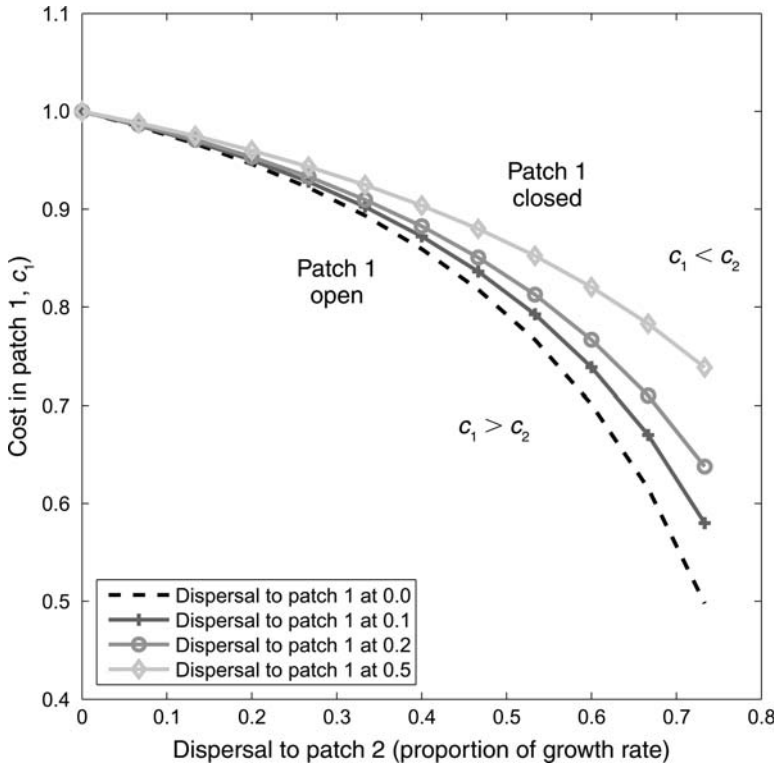

FIG. 4. Density-dependent settlement and critical cost levels for different dispersal rates to patch 1. By holding dispersal to patch 1 (reserve designate in our analysis) fixed at a particular level, we illustrate how the critical cost coefficient changes as the dispersal from patch 1 (reserve designate) to patch 2 (fished area) increases. The area below the critical cost threshold illustrates conditions for which it is optimal to have both patches open to fishing ($c_1 < c_1^{\text{crit}}$) and the area above shows when it is optimal to close patch 1 to fishing ($c_1 \geq c_1^{\text{crit}}$). The lines represent different critical cost coefficients for different assumptions regarding the dispersal flows to patch 1. Unlike in Fig. 2, we do not find cases where the critical cost parameter is lower than the costs in patch 2 (fished area).

that even with a cost coefficient greater than one (all points to the left of the "dispersal cost threshold" line in Fig. 3) but less than the critical cost level ($1 < c_1 < c_1^{\text{crit}}$), it is possible that fishing would be justified optimally in patch 1 when it would not in the case with no connectivity. Thus, dispersal can make fishing profitable in places that would otherwise be unexploited. This case is also evident in the two lower panels of Fig. 2.

The source–sink case illustrated in the upper left panel in Fig. 2 corresponds to the x-axis in Fig. 3. As we increase the dispersal entering patch 2, the critical cost parameter decreases. That is, the economic gains from fish swimming from the high-cost (patch 1) to the low-cost patch (patch 2) more than compensate for the lost returns from closing patch 1. As the dispersal rate increases, this effect increases and for high enough levels, the critical cost parameter may actually be below the operating cost level in patch 2. This occurs for all points to the right of the cost in patch 2 line (identified by c_2) in Fig. 3. In fact, as is illustrated in Fig. 3, it may be profitable to close a patch with very low costs, depending on the dispersal rate, because the closed patch is more valuable as a source for the other patch.

As we move off either axis, the degree of dispersal (mixing) between the two patches depends on the relative optimal density levels and dispersal rates. In the Appendix, Fig. A1 illustrates the net direction of dispersal and its magnitude (measured as a percentage of the aggregate biomass) for each of the triplets (c_1^{crit}, x_1^*, x_2^*) represented in Fig. 3. Essentially, the magnitude of the spillover benefits from closing patch 1 increase as we move from the northwest corner to the southeast corner in Fig. 3.

While a unidirectional source–sink network is the most likely scenario leading to closure as the economically efficient solution, our results imply that more general settings can be candidates for optimal closures. We denote this more general class of systems as net exporters (net sources). It is not sufficient, however, for measured flows to be leaving the closed area for a closure to be economically optimal. The cost of fishing must also be such that given the ecological network, it is more profitable to allow fish to grow in the reserve and disperse to the fished area than to fish in both areas.

We illustrate in Fig. 4 and Fig. 5 the case with juvenile dispersal only or with the d_{ij} set to zero. In Fig. 4, we illustrate how c_1^{crit} varies with dispersal to patch 2,

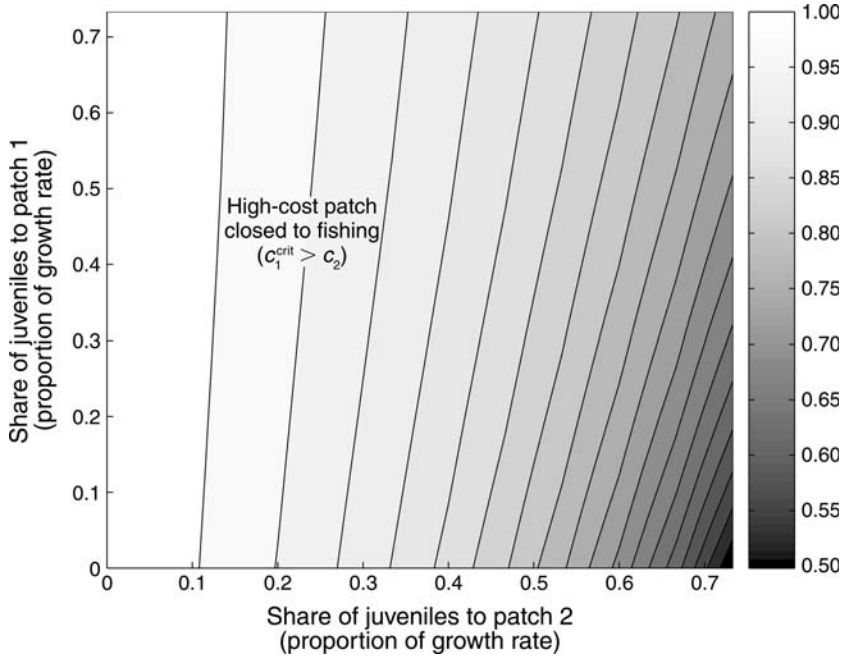

FIG. 5. Density-dependent settlement and critical cost coefficient levels. On both axes, we measure the share of juveniles that move from one patch to another as a proportion of the patch intrinsic growth rates (recall that we impose the adding-up restriction on the juvenile dispersal process). The y-axis corresponds to cases where patch 1 is a sink and the x-axis corresponds to the case where patch 2 is a sink. The contour lines correspond to critical cost coefficients (c_1^{crit}) for which closing patch 1 to fishing is part of the optimal solution. Unlike in Fig. 3, there are no cases in which the critical cost coefficient is lower than the coefficient in patch 2 (fished area).

holding the dispersal to patch 1 fixed at (0, 0.1, 0.2, 0.5). Unlike the above analysis, dispersal in this setting is measured as the share of juveniles produced in patch i settling in patch j. Therefore, as we move away from the origin along the x-axis, for example, we increase the share (b_2) of the juveniles from patch 1 settling in patch 2, but this increase implies that local retention a_1 decreases (recall, we are imposing the constraint that $a_1 + b_2 = 1$).

Both Fig. 4 and Fig. 5 illustrate that, as the dispersal rate into patch 2 increases, the critical cost parameter decreases and vice versa. The reasoning for these effects is the same as with the adult dispersal case. What is different, however, is that the range of costs where a reserve is optimal is smaller for juvenile dispersal (or density-dependent settlement) than for adult dispersal. That is, $c_1^{crit} > c_2$ for all configurations of the parameters (no c_2 line in either Fig. 4 and Fig. 5). Why is this the case?

Moving along the y-axis in Fig. 5, patch 1 is a pure sink and the critical cost parameter for a closure is equal to 1. This is the same level as the closed case. Why is the dispersal-cost threshold effect ($c_1^{crit} > 1$) that prevailed with density-independent settlement not present in this case? For the simple reason that with the population density in patch 1 equal to 1, any potential positive effects on spillover are eliminated due to density dependence (e.g., high levels of mortality in the settlement process).

Fig. A2 in the appendix illustrates the net dispersal at the optimal solution in this system, which is equal to $b_1x_1^* - b_2x_2^*$, and is measured as a percentage of the aggregate optimal biomass density levels. Relative to the adult dispersal case (Fig. A1), the dispersal flows are greater in this system. If the net magnitude of the spillover benefits is larger as measured at the point of departure (not settlement success), then why is the critical cost parameter range smaller? The answer is because of the density dependence in juvenile dispersal. This illustrates rather clearly the issues associated with using increased egg production as a measure of reserve success for species with density-dependent settlement.

Biological growth rates

Advocates for reserves often propose identifying and closing biological hotspots, defined as areas that are believed to be more biologically productive. In our model, we can represent hotspots with higher a_i parameters. To investigate this conjecture, we solve for the critical growth rate in patch 1 such that a closure would be optimal and compare it to the level in the open patch. We do this assuming that the only heterogeneity in the system is in the growth rates (costs are equal at 0.25). If the critical rate is above the level in the open patch, then we can conclude that closing the more biologically productive patch is optimal.

Here we solve for the set (a_1^{crit}, x_1^*, x_2^*) by simultaneously solving Eqs. 3 and 4, and $F_1(x_1, x_2) = 0$ for

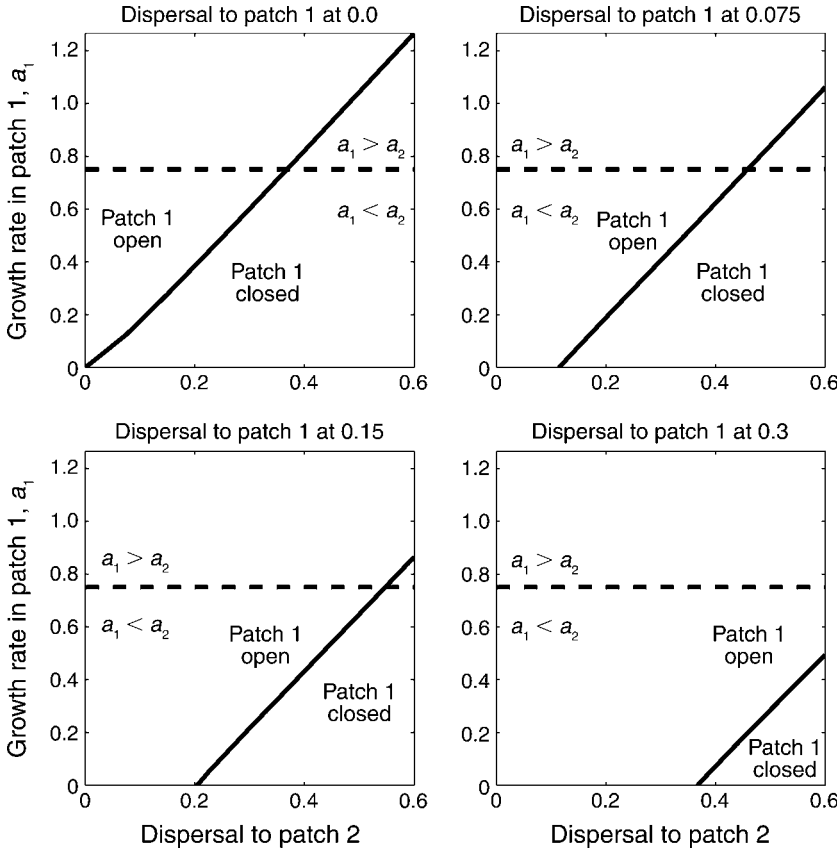

FIG. 6. Density-independent settlement and critical growth rates for different rates of dispersal to patch 1. By holding dispersal to patch 1 (reserve designate in our analysis) fixed at a particular level, we illustrate how the critical growth rate changes as the dispersal from patch 1 (reserve designate) to patch 2 (fished area) increases. We assume that costs are equal across the patches. Regions in the panels illustrate the optimal solution whereby, for example, it is optimal to have both patches open to fishing ($a_1 < a_1^{\text{crit}}$) or to close patch 1 to fishing ($a_1 \geq a_1^{\text{crit}}$). The dashed line represents the critical growth rate in patch 2 (a_2). When the growth rate (solid line) is above the dashed line, it is optimal to close the high-productivity patch. The top left panel represents the case of unidirectional dispersal (patch 1 is a source and patch 2 is a sink). The other panels represent different dispersal rates from patch 2 to patch 1. Points to the left of the intercept on the x-axis are infeasible.

different rates of dispersal. Unlike the cost case, however, there are combinations of dispersal rates that lead to infeasible critical levels with negative growth rates. These are infeasible because there are conditions on the growth and dispersal parameters that need to hold to ensure a positive equilibrium biomass level. For example, when a patch 1 is a pure source (d_{12}, d_{22}, and b_1 are equal to zero), it must be the case that $a_1 > d_{11}$. If $a_1 \leq d_{11}$, then the net intrinsic growth rate would be negative (or zero) leading to zero population levels. In Fig. 7 and Fig. 9, the region with implied negative growth rates is labeled infeasible and the growth rate in the fished area is also labeled (a_2).

As we did with the cost analysis, we begin by presenting the results for the "adult" dispersal case and for a discrete set of dispersal rates to patch 1 (our reserve designate). Fig. 6 illustrates how a_1^{crit} increases with increases in the dispersal rate to patch 2, holding the dispersal rate to patch 1 fixed at (0, 0.075, 0.15, 0.3). The x-axes are now simply the dispersal rate (not measured relative to the growth rate). To compare relative magnitudes of the dispersal rates divide by the critical growth parameters, where the levels are represented either by points (Fig. 6) on the line or by the contour lines (Fig. 7).

Starting with the upper left panel in Fig. 6, which represents the case with patch 1 a source and patch 2 a sink, the critical growth rate increases as the dispersal rate to patch 2 increases. If the actual a_1 is greater than a_1^{crit} and the dispersal rate is low (region above the line), then it is economically optimal for both patches to be open to fishing. If the dispersal rate is high, then closing patch 1 is an economically optimal solution (region below the line). We also illustrate the growth rate assumed in patch 2 (a_2).

Similar to the results for closing the low-cost patch, closing the high biologically productive patch is economically optimal with high dispersal rates to patch 2. This potential outcome is illustrated in all the panels, except the lower right corner in Fig. 6. The intuition for

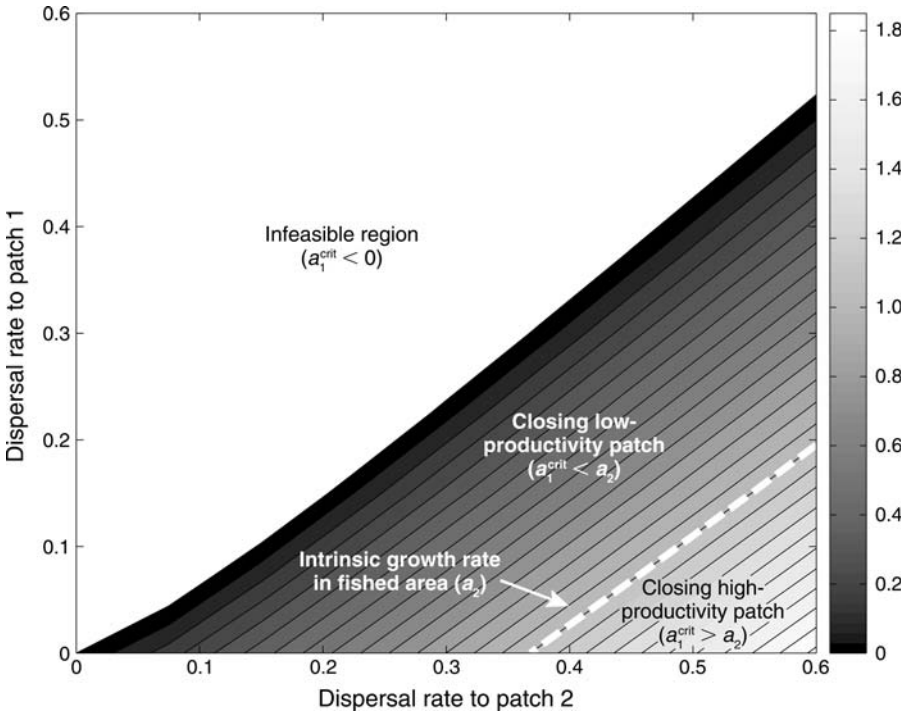

FIG. 7. Density-independent settlement and critical growth rates. The axes are the dispersal rates, d_{ij}. The contour lines correspond to the critical growth rate in patch 1 that would lead to closing patch 1 when the costs in both patches are equal (0.25). Except for the bottom right area, which is delineated by the dashed line, the critical growth rate in patch 1 is below the growth rate in patch 2. For this region, if a closure is optimal, it is more likely to be that the low-growth patch is closed to fishing. Only for high dispersal rates in systems where patch 1 (reserve designate) is acting close to a source do we find that the critical growth rate is higher than in the fished patch.

this result can be seen with the single patch case with logistic growth, where higher growth rates lead to higher yields. In a patchy system, higher growth rates are areas that are more profitable and therefore, the foregone profits (or opportunity costs) from closing these areas are higher. However, when the dispersal from the reserve is sufficient to outweigh these higher returns, it becomes optimal to close the patch with higher growth rates. Sanchirico and Wilen (2002) found a similar result. We do not find this result in the lower right panel, because the net benefits from spillover are not great enough to outweigh the lost profitability. Recall that, with dispersal potentially flowing in both directions, the relative dispersal rates are more important than the absolute levels for setting the optimal catch rates.

Fig. 8 and Fig. 9 illustrate the analysis for the case with juvenile dispersal. The axes measure the share of juveniles contributing to the other patch's growth. Unlike the previous analysis where we analyzed adult and juvenile dispersal separately, we consider both processes simultaneously when mapping out the critical intrinsic growth rate in the presence of juvenile dispersal. The critical intrinsic growth rate we solve for is a_1^0, which is the growth rate when all juveniles are retained locally. Because of the adding up restriction (recall, the unscaled version is $A_i + (B_j/m_j) = a_i^0$ with $m_j = 1$), when we vary the share of juveniles dispersing B_i or B_j, we need to ensure that this constraint is met at each point. In general, solving for this triplet is a highly nonlinear problem and when adult dispersal rates are set to zero, the numerical results are unstable. On the other hand, when adult dispersal is included, the solutions are more easily found. Therefore, we hold the adult dispersal rates fixed and equal across the patches at $d_{ij} = 0.3$. The remaining parameters are the same as the adult dispersal analysis in Fig. 7.

Not surprisingly, the pattern is very similar between Fig. 7 and Fig. 9 with some differences. First, the region where closing the high growth rate patch is the best choice is smaller. See, for example, the upper left panel in Fig. 8. Second, the infeasible region is larger and it now encompasses the origin. It is important to note that, in this case, the reserve is a pure source of juveniles along the x-axis, but it is only a net source with respect to adult dispersal (as determined by the optimal population sizes for x_1^* and x_2^*.

Across the two cases, when the objective is to maximize the present discounted value from fishing, closing patches with high intrinsic growth rates is the optimal policy when the patch is also a net source with high spillover. In an ecosystem context, these appear to be necessary conditions for a patch to be considered a bioeconomic hotspot. Therefore, while it is not always

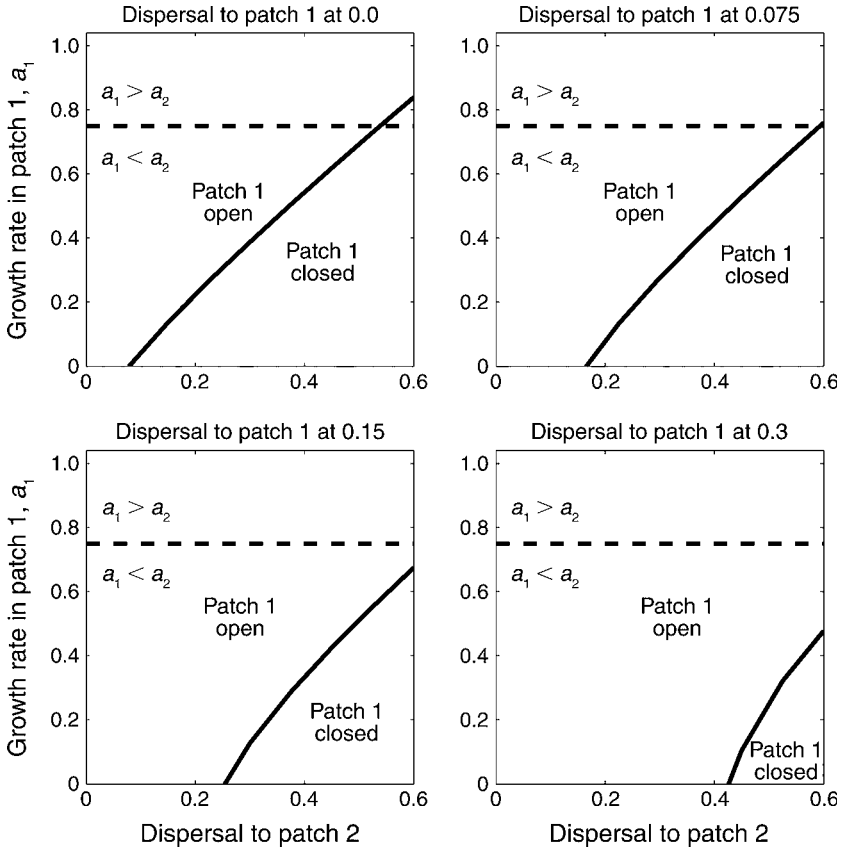

FIG. 8. Density-independent and -dependent settlement and critical growth rates for different dispersal rates to patch 1. By holding the share of juveniles to patch 1(reserve designate) fixed at a particular level, we illustrate how the critical growth rate changes as the share of juveniles from patch 1 (reserve designate) to patch 2 (fished area) increases. Costs are equal across the patches. Regions in the panels illustrate the optimal solution whereby, for example, it is optimal to have both patches open to fishing ($a_1 < a_1^{\text{crit}}$) or to close patch 1 to fishing ($a_1 \geq a_1^{\text{crit}}$). The dashed line represents the critical growth rate in patch 2 (a_2). When the critical growth rate (solid line) is above the dashed line, it is optimal to close the high-productivity patch. The upper left panel represents the case of unidirectional flows of juveniles (patch 1 is a source of larvae and patch 2 is a sink). The other panels represent different levels of larval flows from patch 2 to patch 1. Points to the left of the intercept on the x-axis are infeasible.

optimal to close the high intrinsic growth patch, closing low biological productivity areas might be optimal.

Sensitivity analysis

In most marine systems, the assumption that there is no mortality in the juvenile dispersal process is unrealistic. We investigated this by setting the mortality rates equal to and less than 1 and generating figures similar to those presented. We found that the level of the critical cost parameter is higher and growth rate is lower, everything else being equal. The value associated with the ecological network decreases with increased dispersal mortality. As the dispersal mortality increases, it pays even with higher operating costs to catch the fish before they are subject to the higher mortality, which implies keeping the area open to fishing.

We also investigated the effect of lower discount rates across all cases. Because the lower the discount rate, the higher the optimal population, as illustrated in the closed analytical solution in the Appendix, it is possible that lower discount rates could favor closures. We find increases in the feasible regions for critical costs and growth rates when the analysis is done with a 2% discount rate.

Finally, in the cost analysis, we explore the effects of asymmetries in the biological growth rates and in the growth rate analysis, asymmetries in the operating costs. With respect to the case of asymmetries in biological growth rates, we focus on the case of higher growth rates in the fished area (patch 2) when solving for the critical cost parameters. Due to the opportunity costs associated with higher growth rates, this case is more likely to lead to significant changes in the feasible cost region. The results, however, did not vary significantly from those presented in Figs. 3 and 5. We also considered the case of lower costs in the fished area (patch 2) when solving for the critical growth rates, which again is likely to favor optimal closures. Relative to Fig. 7 and Fig. 9, we find a larger feasible region (smaller infeasible region).

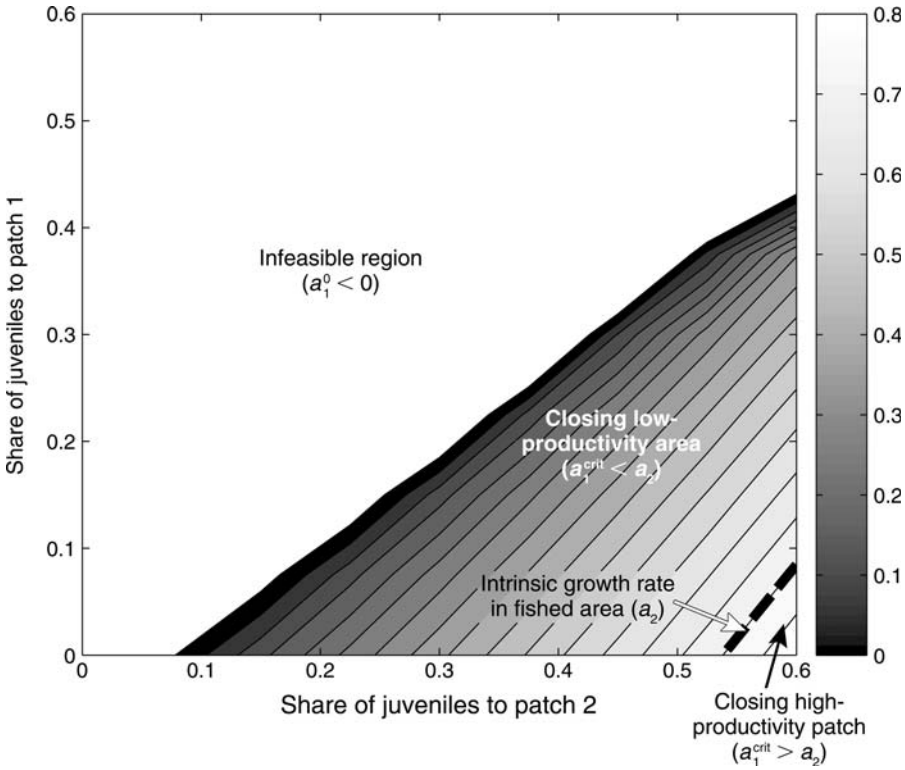

FIG. 9. Density-independent and -dependent settlement and critical growth rates. The axes represent the share of juveniles that disperse from one patch to the other. The contour lines correspond to the critical growth rates a_1^0 that would lead to optimal closures when the costs in both patches are equal (0.25) and adult dispersal rates are equal (0.3). Except for the bottom right area, which is delineated by the dashed line, the low-growth patch is closed to fishing.

CONCLUSIONS

This paper identifies situations where long-term system-wide fishery profits are maximized and where reserves (as opposed to nonzero fishing levels in all patches) emerge as part of the optimal solution. In reality, most fisheries are not optimally managed, since it is difficult to precisely determine population sizes or accurately regulate catch. However, our stylized model does shed light on general conditions whereby reserves are more likely to be politically acceptable, regardless of whether the goal of the reserve is increased catches, biodiversity, or profits.

Intuitively, optimal management of patchy biological systems trades off the loss in profits from a fish leaving, the gain in profit from the fish being caught in another area, and the change in fishing costs due to the reallocation of the stock. An implication is that optimal spatial management requires not just managing the fish stock in each area but the direction and magnitude of dispersal. In this setting, a reserve is simply a way to manage and influence the dispersal to high-profit patches. The evaluation of the trade-offs are based on relative profitability, which depends on relative economic and ecological conditions, and the nature of the dispersal mechanisms.

With respect to optimal no-take zones, the conditions for these to emerge depend on the spatial heterogeneity of the system and dispersal mechanisms. For example, in most situations, the higher cost patch is likely to be closed optimally. Closing lower cost patches, however, can be optimal when the dispersal rate into the fished area is very high and there is little, if any, out migration of biomass from the fished area. This is due to the ecological network effect. Optimal closures are also more likely when the growth rate in the reserve designate is lower than in the fished area, a finding that runs contrary to the popular notion of finding and closing the high biological productive patches.

The specific form of ecological connectivity is another important determinant of our results. Relative to density-dependent settlement, the density-independent system increased the range of parameters for which a complete closure is the optimal solution. This is somewhat surprising, but can be explained by the fact that as the reserve population increases, density-dependent effects become more pronounced and begin to dominate the potential benefits from spillover. Regardless of the mechanism, the range of parameters leading to complete closure increases with increases in the dispersal rate, provided that the reserve is acting as a net exporter.

Our results echo the themes (e.g., Gerber et al. 2003, Guichard et al. 2004) that the key to understanding the optimal spatial management of marine species is knowledge of dispersal, and the causes and timing of density dependence (Forrester and Steele 2000). Unfortunately, both factors are notoriously difficult to estimate for many marine species (e.g., Steele 1997, Shanks et al. 2003). It is for this reason that we undertake qualitative analysis rather than attempt quantitative analysis. Our work also reinforces the idea that efforts made to improve estimates of dispersal and predictive models of density dependence in marine systems may have potentially large payoffs in efficient management.

We emphasize that our assumptions are conservative in the sense that they are more likely to conclude that point A rather than point B in Fig. 1 is the optimal solution. An important area for future research is to understand which of the many dimensions of fishery management, such as bycatch, multispecies interactions, and economic and biological uncertainties (Lauck et al. 1998, Costello and Polasky 2005), could also provide circumstances where marine reserves are optimal. Because ocean management is broader than just fisheries management, it seems prudent to also investigate effects when there exist in situ values to the fish stock, such as when there are nonconsumptive uses. All of these analyses would need to consider the spatial ecology and economics together and would need a foundation from which to compare the results. Our integrated ecological-economic model is an example of such a framework.

As information on the nature and strength of ecological connectivity and patchy environments in marine systems increases, the ability to tailor policies to account for these interactions will increase. In fact, we are likely to move toward a zonal approach, with varying types of uses permitted across zones, with no-take zones and rotating harvest zones as possible uses. A key component in the planning of a zonal system will involve the identification of bioeconomic hotspots that might or might not be good candidates to be closed to all extractive uses. In a spatial system, some of the characteristics of a hotspot, as identified in our analysis, would be a patch that is a net exporter with high dispersal flows out of it, relatively higher cost and with lower biological productivity. Further clarification of how to define and empirically identify these hotpots is an important area for future (interdisciplinary) research. Importantly, as our analysis shows, hotspots are more properly viewed as determined by both biological and economic factors, rather than biological factors alone.

Acknowledgments

We thank seminar participants at the NOAA Library "Brown Bag" seminar series (Silver Spring 2005), NOAA Northwest Science Center "JAM" seminar series (Seattle 2005), Department of Economics, University of Iceland (Reykjavik 2005), and the third workshop on spatial modeling in ecology and economics (Trieste 2005) for their helpful comments. We also very much appreciate the insights of Tim Essington, Ragnar Arnason, and two anonymous reviewers. Funding for this research has been provided by NSF Biocomplexity in the Environment Grant OCE-0119976 (to J. N. Sanchirico, A. Hastings, and U. Maldvakar), and Resources for the Future (to J. N. Sanchirico).

Literature Cited

Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications **8**:S79–S92.

Anderson, L. 2002. A bioeconomic analysis of marine reserves. Marine Resource Economics **15**(3):311–334.

Bernstein, B, S. Iudicello, and C. Stringer. 2004. Lessons learned from recent marine protected area designations in the United States. Report for The National Marine Protected Area Center (NOAA). National Fisheries Conservation Center, Ojai, California, USA.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations, Fishery Investigations: Series 2 Vol. XIX, Her Majesty's Stationary Office, London, UK.

Botsford, L., A. Hastings, and S. Gaines. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecology Letters **4**:144–150.

Botsford, L., F. Micheli, and A. Hastings. 2003. Principles for the design of marine reserves. Ecological Applications **13**: S25–S31.

Brown, G. M., and J. Roughgarden. 1997. A metapopulation model with private property and a common pool. Ecological Economics **22**:65–71.

Carr, M. H., and D. C. Reed. 1993. Conceptual issues relevant to marine catch refuges: examples from temperate reef fishes. Canadian Journal of Fisheries and Aquatic Sciences **50**:2019–2028.

Clark, C. W. 1990. Mathematical bioeconomics. The optimal management of renewable resources. Second edition. John Wiley and Sons, New York, New York, USA.

Costello, C., and S. Polasky. 2005. Spatial bioeconomics under uncertainty. Presented at the Association of Environmental and Resource Economics Summer 2005 workshop, "Natural resources at risk." ⟨http://www.aere.org/meetings/0506workshops.html⟩

Crowder, L., S. Lyman, W. Figueira, and J. Priddy. 2000. Source–sink population dynamics and the problem of siting marine reserves. Bulletin of Marine Science **66**:799–820.

Forrester, G. E., and M. A. Steele. 2000. Variation in the presence and cause of density-dependent mortality in three species of reef fishes. Ecology **81**:2416–2427.

Gerber, L. R., L. W. Botsford, A. Hastings, H. Possingham, S. Gaines, S. Palumbi, and S. Andelman. 2003. Population models for marine reserve design: a retrospective and prospective synthesis. Ecological Applications **13**:S47–S64.

Guichard, F., S. A. Levin, A. Hastings, and D. Siegel. 2004. Toward a dynamic metacommunity approach to marine reserve theory. BioScience **54**:1003–1011.

Halpern, B. 2003. The impact of marine reserves: Do reserves work and does reserve size matter? Ecological Applications **13**:S117–S137.

Hannesson, R. 1998. Marine reserves: What will they accomplish? Marine Resource Economics **13**:159–170.

Hastings, A., and L. W. Botsford. 1999. Equivalence in yield from marine reserves and traditional fishery management. Science **284**:1537–1538.

Hastings, A., and L. W. Botsford. 2003. Comparing designs of marine reserves for fisheries and for biodiversity. Ecological Applications **13**:S65–S71.

Hilborn, R., F. Micheli, and G. De Leo. 2006. Integrating marine protected areas with catch regulation. Canadian Journal of Fisheries and Aquatic Sciences **63**:642–649.

Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences (USA) **100**:6564–6568.

Holland, D. S., and R. J. Brazee. 1996. Marine reserves for fisheries management. Marine Resource Economics **11**:157–171.

Holt, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution, Theoretical Population Biology **28**:181–208.

Huffaker, R. G., M. G. Bhat, and S. M. Lenhart. 1992. Optimal trapping strategies for diffusing nuisance-beaver populations. Natural Resource Modeling **6**:71–97.

Jannmatt, J. A. 2005. Sharing clams: tragedy of an incomplete commons. Journal of Environmental Economics and Management **49**:26–51.

Kamien, M. L., and N. L. Schwartz. 1991. Dynamic optimization the calculus of variations and optimal control in economics and management. Second edition. North-Holland, New York, New York, USA.

Lauck, T., C. W. Clark, M. Mangel, and G. Munro. 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecological Applications **8**: S72–S78.

National Research Council. 2001. Marine protected areas: tools for sustaining ocean ecosystems. National Academy Press, Washington, D.C., USA.

Neubert, M. G. 2003. Marine reserves and optimal harvesting. Ecology Letters **6**(9):843–849.

Pezzey, J. C. V., C. M. Roberts, and B. T. Urdal. 2000. A simple bioeconomic model of a marine reserve. Ecological Economics **33**:77–91.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist **132**:652–661.

Quinn, T. J., II, and R. B. Deriso. 1999. Quantitative fishery dynamics. Oxford, New York, New York, USA.

Rodwell, L., E. Barbier, C. Roberts, and T. McClanahan. 2002. A model of tropical marine reserve-fishery linakges. Natural Resources Modeling **15**(4):453–486.

Sanchirico, J. N. 2004. Designing a cost-effective marine reserve network: a bioeconomic metapopulation analysis. Marine Resource Economics **19**(1):46–63.

Sanchirico, J. N. 2005. Additivity properties in metapopulation models: implications for the assessment of marine reserves. Journal of Environmental Economics and Management **49**(1):1–25.

Sanchirico, J. N., and J. E. Wilen. 2001. A bioeconomic model of marine reserve creation. Journal of Environmental Economics and Management **42**:257–276.

Sanchirico, J. N., and J. E. Wilen. 2002. The impacts of marine reserves on limited-entry fisheries. Natural Resource Modeling **15**(3):380–400.

Sanchirico, J. N., and J. E. Wilen. 2005. Optimal spatial management of renewable resources: matching policy scope to ecosystem scale. Journal of Environmental Economics and Management **50**:23–46.

Shanks, A., B. Grantham, and M. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications **13**:S159–S169.

Skonhoft, A., and J. T. Solstad. 1996. Wildlife management, illegal hunting and conflicts. a bioeconomic analysis. Environment and Development Economics **1**:165–181.

Steele, M. A. 1997. Population regulation by post-settlement mortality in two temperate reef fishes. Oecologia **112**(1):64–74.

Swearer, S. E., J. S. Shima, M. E. Hellberg, S. R. Thorrold, G. P. Jones, D. R. Robertson, S. G. Morgan, K. A. Selkoe, G. M. Ruiz, and R. R. Warner. 2002. Evidence of self-recruitment in demersal marine populations. Bulletin of Marine Science **70**:S251–S271.

Thorrold, S. R., G. P. Jones, M. E. Hellberg, R. S. Burton, S. E. Swearer, J. E. Neigel, S. G. Morgan, and R. R. Warner. 2002. Quantifying larval retention and connectivity in marine populations with artificial and natural markers. Bulletin of Marine Science **70**:291–308.

Tuck, G. N., and H. P. Possingham. 1994. Optimal harvesting strategies for a metapopulation. Bulletin of Mathematical Biology **56**:107–127.

Tuck, G. N., and H. P. Possingham. 2000. Marine protected areas for spatially structured exploited stocks. Marine Ecology Progress Series **192**:89–101.

Warner, R. R., and R. K. Cowen. 2002. Local retention of production in marine populations: evidence, mechanisms, and consequences. Bulletin of Marine Science **70**:S245–S249.

APPENDIX

Solution techniques, optimal biomass levels, and dispersal flows. (*Ecological Archives* XXXX-XXX-XX).