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DISPERSAL PER RECRUIT: AN EFFICIENT METHOD FOR ASSESSING SUSTAINABILITY IN MARINE RESERVE NETWORKS

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Abstract. Marine reserves are an increasingly important tool for the management of marine ecosystems around the world. However, the effects of proposed marine reserve configurations on sustainability and yield of populations are typically not estimated because of the computational intensity of direct simulation and uncertainty in larval dispersal and density-dependent recruitment. Here we develop a method for efficiently assessing a marine reserve configuration for persistence and yield of a population with sedentary adults and dispersing larvae. The method extends the familiar sustainability criteria of individual replacement for single populations based on eggs-per-recruit (EPR) to spatially distributed populations with sedentary adults, a dispersing larval phase, and limited carrying capacity in the settlement–recruit relationship. We refer to this approach as dispersal-per-recruit (DPR). In some cases, a single DPR calculation, based on the assumption that post-settlement habitat is saturated (i.e., at maximum recruitment), is sufficient to determine population persistence, while in other cases further iterative calculations are required. These additional calculations reach an equilibrium more rapidly than a full simulation of age- or size-structured populations. From the DPR result, fishery yield can be computed from yield-per-recruit (YPR) at each point. We assess the utility of DPR calculations by applying them to single reserves, uniformly distributed systems of reserves, and randomly sized and spaced systems of reserves on a linear coastline. We find that for low levels of EPR in fished areas (e.g., 10% or less of the natural, unfished EPR when post-settlement habitats are saturated by 35% of natural settlement), a single DPR calculation is sufficient to determine persistence of the population. We also show that, in uniform systems of reserves with finite reserve size, maximal fisheries yield occurs when the density of reserves is such that all post-settlement habitat is nearly saturated with settlers. Finally, we demonstrate the application of this approach to a realistic proposed marine reserve configuration.

Key words: *dispersal; fisheries; management; marine reserves; modeling; sustainability.*

Introduction

Recently, there have been efforts in many parts of the world to implement systems of marine reserves for the conservation of marine ecosystems and the management of commercially important fish populations (e.g., Hockey and Branch 1997, Roberts et al. 2001, Norse et al. 2003). While the scientific understanding of the effects of marine reserves on populations has notably improved in recent years (e.g., Lubchenco et al. 2003 and references therein), the design of effective systems of marine reserves remains a challenge (Sale et al. 2005). The selection of marine reserve configurations often focuses on choosing the desired mix of habitat and species in the most efficient way through siting algorithms (e.g., Leslie et al. 2003), while questions of whether fish populations will in fact be sustained in that system of reserves and how the reserves will affect fishery yield are often ignored. It is presumed that since reserves add areas with no fishing, and spawning biomass in such areas often, though not always, increases (Halpern 2003, Micheli et al. 2004), population persistence will necessarily increase as well. Total biomass may not increase, either in the short run if effort displaced from reserves shifts to fished areas (Smith and Wilen 2003, Halpern et al. 2004) or in the long run if fishing effort or landings are not controlled. There is a clear need for assessment of whether the populations within proposed reserves will continue to persist, both at existing harvest rates and potentially higher future rates. However, full two-dimensional model simulations of the effects of marine reserves on persistence are computationally intensive and would be plagued by large uncertainties surrounding the larval and recruitment phases of marine species (e.g., Caley et al. 1996, Hixon et al. 2002). To address these difficulties, we have developed a method for rapidly assessing the effects of a system of marine reserves on a population with sedentary adults and widely dispersing larvae. The

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method requires minimal initial information and has relatively few underlying assumptions.

In conventional (i.e., non-spatial) fisheries management, tools exist for evaluating sustainability and yield of a single, well-mixed, closed fish population in spite of uncertainty in the relationship between egg production by adults and recruitment of young individuals into the adult population (i.e., the stock–recruitment relationship). The effect of fishing on reproduction is expressed in terms of eggs-per-recruit (EPR), which is the number of eggs an average recruit produces over its lifetime (Goodyear 1993). EPR is often approximated as spawning stock biomass per recruit. The effect of fishing on yield is expressed in terms of the yield an average individual provides to the fishery over its lifetime, known as yield-per-recruit (YPR; Beverton and Holt 1957). These indices of the fishery's state are independent of the stock–recruit relationship, and thereby allow reasonably certain statements to be made regarding the effects of fishing on the population without incurring the uncertainty associated with the larval and recruitment phases. However, they require some means of assuring that the fishing rates and size limits chosen to produce a desired level of EPR and YPR will lead to a sustainable population.

The condition for long-term sustainability can be obtained from a model with age structure and density-dependent recruitment. It has been shown that the minimum value of EPR required for persistence of a single, closed population is related to the form of the stock–recruitment relationship at low population levels (Sissenwine and Shepherd 1987, Goodyear 1993). For a single, closed fish population with density-dependent recruitment, this condition translates to the following (Sissenwine and Shepherd 1987):

$$\text{EPR} > \frac{1}{R'(0)} \tag{1}$$

where $R(E)$ is the density-dependent relationship between the number of eggs produced and the consequent number of recruits to the adult population, and $R'(0)$ is the slope of that egg–recruit relationship at the origin. If egg production is reduced by fishing to the point that EPR is less than $1/R'(0)$, the equilibrium population size is 0 (i.e., collapse will occur). Note that Eq. 1 has the same form as the classical condition on lifetime reproduction in models without density-dependence (i.e., $R_0 > 1$), and it has the same replacement interpretation: populations will increase only when individuals reproduce more than enough to replace themselves (Caswell 2001).

The application of Eq. 1 is limited by the difficulty of accurately determining the slope of the egg–recruitment relationship at low abundance (i.e., $R'(0)$). Rather than determining the critical value of EPR for each species, fishery biologists convert EPR to the Spawning Potential Ratio (SPR), the fraction of natural, unfished EPR for which collapse is unlikely to occur (Goodyear 1993),

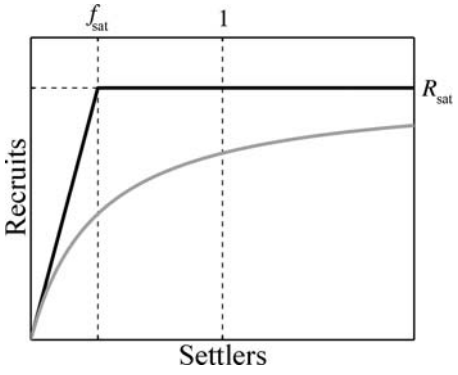

FIG. 1. Density-dependent relationship between recruits and settlers. The number of settlers is plotted in units of the natural settlement level. The solid black curve is a hockey-stick stock–recruitment relationship for which the locations of the natural settlement level (indicated by the "1"), f_{sat} (the fraction of natural settlement that saturates post-settlement habitats), and R_{sat} (the maximum recruitment level) are indicated by the dashed lines. The solid gray curve is a Beverton-Holt stock–recruitment relationship with the same slope at the origin and maximum recruitment level as the hockey-stick stock–recruitment curve.

implicitly assuming that this fraction is constant, at least among similar species and habitats. Based on the analysis of stock and recruit data, as well as modeling studies involving optimization of yield, target values of SPR used for fisheries management are typically in the range of 35–50% (Mace and Sissenwine 1993, Myers and Mertz 1998, Clark 1999, 2002, Myers et al. 1999, Ralston 2002). Thus, the fraction of natural EPR remaining with the effects of fishing, which depends on the mortality and reproductive rates of adults, is used as a gauge of population state (i.e., persistence) in the absence of precise information regarding the form of the stock–recruitment relationship.

While EPR is quite useful for managing single populations, it cannot be used to address persistence with marine reserves because the ultimate consequences of reserves for persistence depend on larval dispersal between populations, and reproductive capacity is not uniform over space. However, for a semelparous marine population with dispersing larvae, uniformly spaced marine reserves along an infinite coastline and complete removal by fishing between the reserves, Botsford et al. (2001) developed a method (their ad hoc method) of estimating whether populations would be sustainable. They assumed that the density dependence in recruitment occurred at the point of settlement and there was a "hockey-stick" relationship (i.e., one that increases linearly until a maximum value is reached and then is constant; see Barrowman and Myers 2000) between settlers and recruits (i.e., between the number of individuals arriving at the adult habitat and the number of individuals that actually enter the adult population; Fig. 1). This form of density-dependent recruitment adequately describes many benthic invertebrates and

reef-dwelling fish with limited post-settlement habitat (Caddy 1986, Wahle and Steneck 1991, Caley et al. 1996). Their method initially assumed that all reserve areas received enough larvae to saturate the post-settlement habitat. As a consequence, there would be maximum larval output from each point within reserves. They then tested the level of potential settlers at a point (i.e., the number of settlers dispersing to that point from all points within reserves) to see if there was enough settlement to saturate the habitat. The level of settlement required was taken to be the same replacement factor required for persistence in conventional, non-spatial management (e.g., 35%). If the post-settlement habitat was indeed saturated at all points inside reserves, the original assumption of maximum larval output was valid, and therefore, it was concluded that the population would persist.

Here we extend that approach to develop a method for estimating the equilibrium spatial structure of a population produced by a system of marine reserves for non-semelparous populations. This method replaces the calculation of EPR in the single population case with a calculation of dispersal-per-recruit (DPR) for the spatially explicit case. DPR is the larval settlement pattern over space that would result from a specified spatial pattern of recruitment. The calculation makes use of the value of EPR at each point and the dispersal pattern from each point. For the initial spatial pattern of recruitment, we assume that all locations receive sufficient settlers to saturate the post-settlement habitat, and therefore, all areas have the maximum number of recruits. This initial assumption is then used to compute the consequent settlement at each point, termed $\mathrm{DPR}_{\mathrm{sat}}$. This settlement value at each point is then tested to determine whether it exceeds the threshold level of settlement required for persistence at that point (e.g., 35% of natural settlement). If $\mathrm{DPR}_{\mathrm{sat}}(\mathbf{x})$ exceeds the threshold at every point, $\mathbf{x}$, implying that recruitment is at saturation levels everywhere, then the initial assumption is met and the population will persist. In cases where this single calculation does not produce a definitive answer regarding persistence of the population over space, multiple iterative applications of the procedure can be used to determine the equilibrium state. We show here that multiple iterations of DPR lead to the spatially explicit equilibrium settlement level much more efficiently than full simulations of populations with age or size structure. Once the equilibrium levels of recruitment have been estimated, a simple additional calculation can be used to determine equilibrium yield.

After defining the calculation of DPR, we assess the utility of single and multiple DPR iterations by investigating marine reserve configurations on an infinite linear coastline. We begin by examining single, isolated reserves, then proceed to systems of uniformly spaced, equal-sized reserves, and finally, address systems of randomly sized and spaced reserves. In each case, our focus is on if and when persistence can be efficiently determined from a single DPR calculation. We also examine the dependence of yield in uniform systems of reserves on the size and density of marine reserves.

To illustrate the use of this method in more realistic scenarios, we then analyze a proposed marine reserve configuration on a finite coastline. We include in this assessment of a realistic marine reserve network the types and levels of information that are generally available in locations with a well-developed resource management capability. In such areas, the pre-reserve level of fishing is often known and the ultimate fishing rate outside reserves can be estimated. The spatial distribution of habitat is also often available and can be accounted for in the assessment. Larval dispersal patterns of the species involved are generally not known in detail, but there is likely to be a range of estimated dispersal distances (e.g., Shanks et al. 2003, Kinlan et al. 2005). Therefore, we use the simplest dispersal function that has a variable spatial scale and assess sustainability for a range of likely values. Because of the associated uncertainties, especially in the dispersal patterns, we do not view this assessment as a prediction in the usual sense. It is rather a method for providing guidance regarding the relative contribution to sustainability of proposed marine reserve network designs.

Methods

Dispersal per recruit (DPR)

We derived the DPR method in a continuous space of arbitrary dimensionality (typically one or two dimensions), but it could also be formulated in discrete space by appropriate replacement of integrals with summations. If one initially assumes that all locations, whether in reserves or not, are saturated with recruits and are at equilibrium, then one can calculate the corresponding level of egg production based on the EPR at each location:

$$E_{\mathrm{sat}}(\mathbf{x}) = \mathrm{EPR}(\mathbf{x}) \cdot R_{\mathrm{sat}}(\mathbf{x}) \tag{2}$$

where $R_{\mathrm{sat}}(\mathbf{x})$, $\mathrm{EPR}(\mathbf{x})$, and $E_{\mathrm{sat}}(\mathbf{x})$ are the recruitment level at saturation of the post-settlement habitat (from now on simply referred to as habitat saturation), the EPR, and the corresponding annual egg production at location $\mathbf{x}$, respectively. Given this level of egg production, one can use the dispersal pattern, which connects egg production at one location to post-larval settlement at another, to determine settlement over space:

$$\begin{aligned}\mathrm{DPR}_{\mathrm{sat}}(\mathbf{x}) &= \int_{\Omega} D(\mathbf{x}, \mathbf{y}) \cdot E_{\mathrm{sat}}(\mathbf{y})\, d^N y \\ &= \int_{\Omega} D(\mathbf{x}, \mathbf{y}) \cdot \mathrm{EPR}(\mathbf{y}) \cdot R_{\mathrm{sat}}(\mathbf{y})\, d^N y \end{aligned} \tag{3}$$

where N is the number of spatial dimensions, Ω represents the habitat area over which the integration is performed, $D(\mathbf{x}, \mathbf{y})$ is the probability density that eggs produced at $\mathbf{y}$ settle at $\mathbf{x}$, and $\mathrm{DPR}_{\mathrm{sat}}(\mathbf{x})$ is the density of

settlers at $\mathbf{x}$ that would result from habitat saturation everywhere, calculated as the sum of larvae dispersed to that location from all possible origins. The number of settlers at each location (i.e., $\mathrm{DPR}_{\mathrm{sat}}(\mathbf{x})$) can then be tested to determine whether it is greater than the settlement level presumed necessary for habitat saturation, and therefore, whether the initial assumption was valid.

Note that the habitat saturation level, $R_{\mathrm{sat}}(\mathbf{x})$, is only important in a relative sense. As one ultimately compares DPR with natural settlement levels to determine whether the fraction of natural settlement arriving at each location is sufficient to ensure habitat saturation, only values relative to natural levels are relevant. In particular, if all locations are assumed equally suitable for recruitment and reproduction (i.e., $R_{\mathrm{sat}}(\mathbf{x})$ and natural $\mathrm{EPR}(\mathbf{x})$ are independent of $\mathbf{x}$), then a simplified habitat saturation condition can be derived from Eq. 3:

$$\frac{\mathrm{DPR}_{\mathrm{sat}}(\mathbf{x})}{\mathrm{NEPR}\cdot R_{\mathrm{sat}}} = \frac{\displaystyle\int_{\Omega} D(\mathbf{x},\mathbf{y})\cdot \mathrm{EPR}(\mathbf{y})\, d^N y}{\mathrm{NEPR}} = \int_{\Omega} D(\mathbf{x},\mathbf{y})\cdot \mathrm{FNEPR}(\mathbf{y})\, d^N y > f_{\mathrm{sat}} \qquad (4)$$

where NEPR is the natural EPR level, $\mathrm{FNEPR}(\mathbf{x})$ is the fraction of natural EPR remaining after fishing at $\mathbf{x}$, and f_{sat} is the fraction of natural settlement needed for habitat saturation. With these simplifying assumptions, the habitat saturation condition reduces to a test of whether the number of settlers dispersed to a location over the lifetime of an individual recruit at each location is greater than some fraction of the natural settlement level. However, the assumption that all locations are equally suitable for recruitment and reproduction is not required by the method.

DPR_n: an iterative approach to determining the equilibrium population

The calculation of $\mathrm{DPR}_{\mathrm{sat}}(\mathbf{x})$ described thus far is a test of habitat saturation over space that reflects equilibrium settlement levels in some situations and is independent of the typically uncertain form of the settler–recruitment relationship. However, it does not determine the ultimate equilibrium state of the population when some locations are not habitat saturated. In these situations, a full simulation of the population could be used. Fortunately, the definition of $\mathrm{DPR}_{\mathrm{sat}}$ suggests a simpler iterative approach to determining the equilibrium state of the population that does not require keeping track of a detailed size and/or age structure for the adult population. As with a full simulation of the population, this approach requires a functional form for the settler–recruitment relationship. Just as habitat saturation served as an initial assumption for the recruitment level, one can use the recruitment level derived from the settler–recruitment relationship and the number of settlers calculated in $\mathrm{DPR}_{\mathrm{sat}}(\mathbf{x})$ as an initial recruitment level:

$$R_1(\mathbf{x}) = g_{\mathbf{x}}(\mathrm{DPR}_{\mathrm{sat}}(\mathbf{x})) = g_{\mathbf{x}}\left(\int_{\Omega} D(\mathbf{x},\mathbf{y})\cdot \mathrm{EPR}(\mathbf{y})\cdot R_{\mathrm{sat}}(\mathbf{y})\, d^N y\right) \qquad (5)$$

where $R_1(\mathbf{x})$ is the recruitment level and $g_{\mathbf{x}}$ is the settler–recruit relationship at $\mathbf{x}$. This recruitment level can then be used to determine a corresponding egg production at each location based on the assumption that each recruit produces EPR eggs over its lifetime and that each location is at the constant-recruitment age distribution (i.e., the adult distribution that would result after long time periods from constant recruitment and a fixed fishing pressure). Using the dispersal pattern and the settler–recruit relationship, recruitment can be predicted from this egg production. This procedure can be iterated so that

$$R_m(\mathbf{x}) = g_{\mathbf{x}}(S_m(\mathbf{x})) = g_{\mathbf{x}}\left(\int_{\Omega} D(\mathbf{x},\mathbf{y})\cdot \mathrm{EPR}(\mathbf{y})\cdot R_{m-1}(\mathbf{y})\, d^N y\right) \qquad (6)$$

where $R_m(\mathbf{x})$ and $\mathrm{DPR}_m(\mathbf{x})$ are the recruitment and settlement levels for the mth iteration, respectively, $R_0(\mathbf{x}) = R_{\mathrm{sat}}(\mathbf{x})$, and $\mathrm{DPR}_1(\mathbf{x}) = \mathrm{DPR}_{\mathrm{sat}}(\mathbf{x})$, i.e., the "saturation settlement" at $\mathbf{x}$ as defined in the previous section.

This iterative approach converges on the true equilibrium levels of recruitment, egg production, and settlement for any nonnegative dispersal pattern (i.e., $D(\mathbf{x},\mathbf{y}) \geq 0\ \forall\ \mathbf{x},\mathbf{y}$) and any nondecreasing settler–recruit relationship that has a maximum recruitment level. First, note that the series of recruitment values are bounded,

$$0 \leq R_m(\mathbf{x}) \leq R_{\mathrm{sat}}(\mathbf{x}) \quad \forall\, \mathbf{x} \qquad (7)$$

because recruitment is nonnegative and the settler–recruit relationship has a maximum value. The series are also nonincreasing:

$$R_{m+1}(\mathbf{x}) \leq R_m(\mathbf{x}) \quad \forall\, \mathbf{x}. \qquad (8)$$

This is true for $m = 0$ because $R_0(\mathbf{x}) = R_{\mathrm{sat}}(\mathbf{x})$. The result follows for other values of m from the fact that the settler–recruit relationship is nondecreasing and the dispersal matrix is positive semi-definite. Therefore, the series must converge as any decreasing, bounded infinite set of numbers converges (Rubin 1976). Let us denote the values the series converge to by $R_\infty(\mathbf{x})$. Then we have

$$R_\infty(\mathbf{x}) = g_{\mathbf{x}}\left(\int_{\Omega} D(\mathbf{x},\mathbf{y})\cdot \mathrm{EPR}(\mathbf{y})\cdot R_\infty(\mathbf{y})\, d^N y\right). \qquad (9)$$

This relationship is the definition of an equilibrium point of the original model, and therefore, the series must converge to a valid equilibrium state of the system.

It is worth noting that DPR_n will not necessarily converge on the equilibrium state occupied by a real

system, particularly if the system begins with an extremely low number of individuals, as might occur after heavy fishing. It is conceivable that the settler–recruit function has multiple inflection points (e.g., Allee effects) and, therefore, multiple stable equilibria. In this case, DPR_n will converge on the highest stable equilibrium, but the true population could converge on a lower stable equilibrium if there are initially few individuals. However, it is possible to search for other stable equilibria using this method by setting the initial recruitment value at a small value. By a similar logic to that used above, it can be shown that the series will always converge on the nearest stable equilibrium.

In essence, DPR_n reduces the problem of finding the equilibrium state of the full model to an equivalent problem for a semelparous fish population (with the recruitment level being equivalent to the "adult population" of the semelparous population). As such, many of the results related to equilibrium states of semelparous populations can also be applied to DPR_n (e.g., VanKirk and Lewis 1997) and the convergence of DPR_n for suitable settler–recruit relationships can be seen as a result of the global stability of the equilibrium of these systems (Hardin et al. 1990). It should be noted, however, that DPR_n only predicts the equilibrium state of the population, and any nonequilibrium dynamics that occur in the semelparous population, such as the chaotic dynamics in semelparous populations with a Ricker stock–recruitment relationship (which would violate the condition that the settler–recruit relationship be nondecreasing), may not be seen in the full population model.

Spatial patterns of yield from a fishery that would result from a system of reserves can be calculated from the values of equilibrium recruitment derived from DPR_n given the yield-per-recruit (YPR):

$$Y_\infty(\mathbf{x}) = \mathrm{YPR}(\mathbf{x}) \cdot R_\infty(\mathbf{x}) \tag{10}$$

where $Y_\infty(\mathbf{x})$ is the equilibrium yield at location $\mathbf{x}$.

Full model for comparison

We demonstrate the utility of DPR_{sat} and DPR_n for studying the effects of spatial management using a simple fisheries model of an age-structured population. While the detailed age structure of the population is not essential to the results, it is worth noting that the model is in discrete time and has 30 age classes with the last age being a plus class. All individuals become reproductively mature at age five, after which fecundity is constant. Individuals experience a natural mortality rate of 0.1/yr throughout their lives, and sexually mature individuals are subject to fishing mortality. The effects of fishing will generally be expressed in terms of the fraction of natural EPR (FNEPR) remaining in a population fished at a given rate, with a FNEPR of 1.0 corresponding to an unfished population and a FNEPR of 0.0 representing an infinite fishing rate (often referred to as the "scorched earth" condition). Yield is calculated based on a von Bertalanffy growth function and a cubic length to weight relationship.

A hockey-stick stock–recruitment function (Barrowman and Myers 2000) will be used to describe the relationship between the number of settlers a location receives and the subsequent number of recruiting juveniles to that location (Fig. 1). This function increases linearly for small values of settlement until it reaches a certain settlement level, after which recruitment is constant. This creates a threshold value of EPR necessary for persistence, below which a single, closed population will collapse (i.e., from Eq. 1, $\mathrm{EPR} > 1/R'(0) \equiv \mathrm{NEPR} \cdot f_{sat}$ which implies that $f_{sat} < \mathrm{FNEPR}$ for persistence). The same settler–recruit relationship will be used for all locations. This is a reasonable assumption given the lack of available fisheries data for parameterizing a spatially varying settler–recruit relationship. The settler–recruit relationship has been parametrized so that a single, closed population collapses when the fraction of natural EPR remaining after fishing is 0.35 (i.e., $f_{sat} = 0.35$; cf. Mace and Sissenwine 1993, Clark 2002). This collapse point has been chosen as representative and is not meant to refer to any particular species. The overall pattern of the results presented below is not sensitive to the precise value of the collapse point.

As the settler–recruit relationship is assumed to be spatially uniform in this model, the habitat saturation condition can be simplified as in Eq. 4. Therefore, for simplicity, we will refer to the left-hand side of Eq. 4 as $DPR_{sat}(\mathbf{x})$ when discussing the results of this model so that these results might be directly compared to f_{sat} without reference to the recruitment level at saturation and the natural, unfished reproductive capacity.

Habitat is presumed to lie along a linear coastline. Adults are sedentary in the model, but larvae disperse over a specified spatial scale. The fraction of larvae produced in one location that settles in another location is given by a Laplacian distribution:

$$p(x, y) = \frac{e^{-|x-y|/a}}{2a} \tag{11}$$

where a is the mean dispersal distance. While this is a simplified dispersal function, it allows us to examine the effects of the spatial scale of dispersal on population dynamics. The results are not highly dependent on the exact form or kurtosis of the dispersal pattern, as long as it is symmetric around the point of production and has the specified mean dispersal distance (Lockwood et al. 2002). Dispersal distances in nature vary among species and are typically between 0 and 100 km (Shanks et al. 2003, Kinlan et al. 2005).

To assess the utility of the DPR method for determining persistence in populations with the characteristics described above, we apply it to a number of different marine reserve configurations with varying levels of fishing pressure in non-reserve areas. Fishing effort is assumed to be evenly distributed in non-reserve areas. We begin with a single, isolated reserve on an infinite coastline,

which illustrates the basic functioning of the model system and DPR. Both "scorched earth," in which fishing is assumed to remove all reproductive females from the population (i.e., FNEPR = 0), and nonzero reproduction in fished areas (i.e., FNEPR > 0) are considered. We then proceed to systems of uniformly spaced, equal-sized reserves (hereafter, referred to as "uniform systems of reserves") on an infinite coastline to examine the utility of DPR for predicting persistence and equilibrium population levels in networks of marine reserves.

We then consider systems with five variably spaced and sized reserves occupying a fixed fraction of the total habitat on a periodic coastline to assess the robustness of our conclusions regarding the utility of DPR in more realistic systems with nonuniform distributions of reserves. Reserve size was randomly determined, with the conditions that no reserve could be smaller than the underlying spatial discretization (1/800th of the habitat area) and that the total area in reserves be equal to a given fraction of the coastline. The reserves were then randomly placed along the coast, with the condition that they be nonoverlapping. We considered 100 reserve configurations for each fraction of the coastline in reserves, from which probabilities of persistence were calculated.

Finally, we used the DPR method to assess a realistic marine reserve configuration on a finite coastline that included habitat quality as a demonstration of how this method might be applied for making management decisions. The habitat map is based on the distribution of shallow (0–30 m depth) rocky-bottom habitat along the central coast of California. The marine reserve configuration is similar to those proposed recently for the central coast of California. These reserve and habitat maps were then divided into 2 km wide latitudinal bins and placed on a linear coastline, where bins containing any reserve or habitat areas being labeled as a reserve and/or habitat bin, respectively. FNEPR was assigned three different levels along the coastline. Non-habitat areas were assumed to have a FNEPR of zero, while habitat areas in reserves had a FNEPR of one. Habitat areas outside of reserves were assigned an FNEPR of 0.2, which is comparable to the residual reproductive capacity in a number of California rockfish (O'Farrell and Botsford 2005; FNEPR is essentially the same as the term "fraction of lifetime egg production" [FLEP] used in that study). A number of dispersal distances, ranging from 1 km to 25 km, were considered to take into account uncertainty in the mean dispersal distance.

Results

One important result that follows from the definition of DPR is that if DPR_{sat} indicates that all locations are habitat saturated, then DPR_{sat} gives the true equilibrium level of settlement in a single step. Since the initial assumption is met in this case, recruitment is known at all locations (i.e., all locations receive the maximum amount of recruits) and egg production and settlement follow from Eq. 1 and the dispersal matrix.

A somewhat academic, but informative application of this result is the case of a system of reserves with no reproduction outside of reserves (i.e., the scorched earth condition). This configuration is useful for determining the viability of the reserve system under the worst of all possible fishing conditions outside of reserves. In this case, settlement in non-reserve areas is immaterial for persistence of the population as no reproduction occurs there. If DPR indicates that all reserve areas are saturated with larvae (i.e., $DPR_{sat}(\mathbf{x}) > f_{sat}(\mathbf{x})$ inside reserves), then the population persists and DPR gives the equilibrium state of the population. This simple test for global persistence from DPR is valid no matter what the size or configuration of reserves.

DPR applied to a single isolated reserve along an infinite linear coastline

It has been shown that a population will persist in an isolated reserve with no reproduction outside the reserve (i.e., scorched earth) if the dispersal distance is on the order of the reserve width or smaller (Botsford et al. 2001). Here we relate this conclusion regarding population persistence to the DPR calculation.

Three possible outcomes exist for DPR for an isolated reserve with scorched earth outside the reserve: (1) $DPR_{sat} > f_{sat}$ *throughout* the reserve; (2) $DPR_{sat} < f_{sat}$ in all areas; and (3) $DPR_{sat} > f_{sat}$ in *some* parts of the reserve, but not in others. If the dispersal distance is small compared to reserve width (thick-dashed curve in Fig. 2a), sufficient larvae will remain inside the reserve to saturate habitat at all reserve locations. Persistence is guaranteed in this case and $DPR_{sat}(\mathbf{x})$ gives the exact equilibrium settlement level. If dispersal distance is large compared to the size of the reserve (thin-solid red and dot-dashed red curves in Fig. 2a), export of larvae outside of the reserve is so high that DPR_{sat} is less than f_{sat} in all locations. In this case, our initial assumption of habitat saturation is invalid, and DPR indicates that the reserve population will collapse, as at least some locations must be saturated with larvae for persistence.

At intermediate dispersal distances (e.g., thin-dashed black curve and thick-solid red curve in Fig. 2a), DPR_{sat} may indicate that some areas of the reserve are saturated with larvae, while others are not. In this case, the final equilibrium state can only be determined by running the full model to equilibrium or iterating DPR (i.e., calculating DPR_n). In our model, at a dispersal distance equal to 0.9 times the width of the reserve (thin-dashed black curve of Fig. 2a), the population persists, but at a dispersal distance of 1.1 times the reserve width (thick-solid red curve in Fig. 2a), the population collapses.

When the FNEPR in fished areas is nonzero, the reserve population will persist at larger dispersal distances than it would in the absence of larval production in fished areas (Botsford et al. 2001). However, as long as FNEPR in fished areas is less than f_{sat}, there will always be a dispersal distance beyond which the population will collapse.

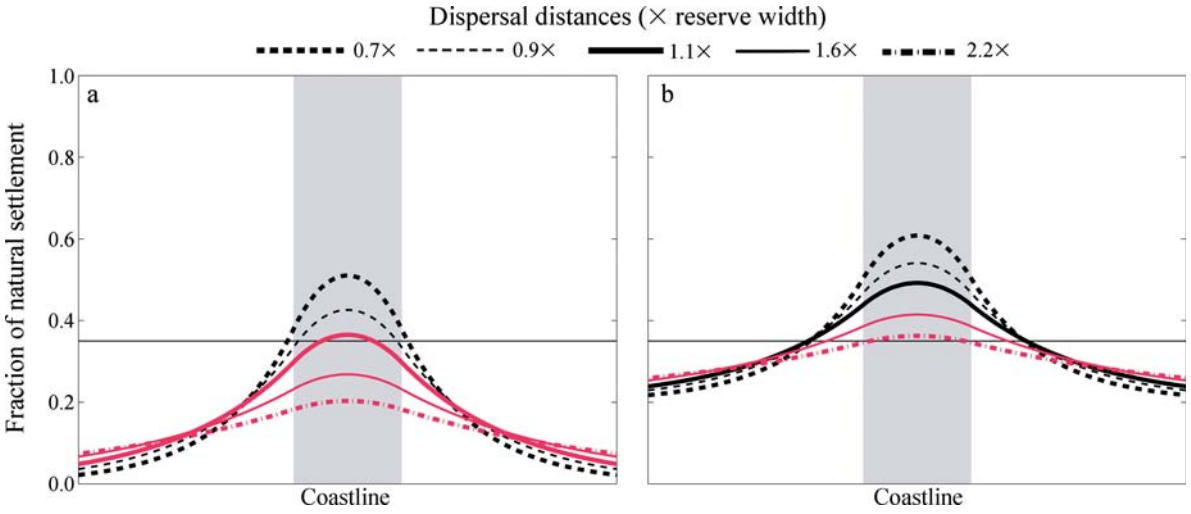

FIG. 2. Recruitment levels assuming saturation by settlers of all post-settlement habitat areas ($DPR_{sat)}$ for several dispersal distances (0.7, 0.9, 1.1, 1.6, and 2.2 times the width of the reserve) in a system with a single, isolated reserve with the fraction of natural eggs-per-recruit (FNEPR) of (a) 0.0 and (b) 0.2 in fished areas. The reserve location is shown in gray. Curves in black indicate persistent populations, while those in red are populations that will collapse. The horizontal line indicates the level of settlement that saturates the post-settlement habitat.

The same three possible outcomes for DPR_{sat} exist when FNEPR is nonzero, though their consequences for persistence are different. For sufficiently large dispersal distances, DPR_{sat} is less than f_{sat} in all areas and collapse will occur. For sufficiently small dispersal distances, DPR_{sat} exceeds f_{sat} inside the entire reserve, but this may not guarantee persistence. When FNEPR in fished areas is sufficiently large (e.g., FNEPR = 0.2, as in Fig. 2b), collapse can occur even if DPR_{sat} is greater than f_{sat} inside reserves (e.g., thin-solid, red curve in Fig. 2b). As sustainability and DPR_{sat} levels inside reserves now depend, to a certain degree, on larvae produced in fished areas that settle in reserve areas, the level of DPR in fished areas cannot be ignored when determining persistence.

DPR_n can be used to rapidly determine the equilibrium state of the population in indeterminate cases, but the functional form for the settler–recruit relationship must be known or assumed (Fig. 3). When there is a stable nonzero population, DPR_n rapidly converges on the equilibrium state and the initial DPR_{sat} calculation is an acceptable approximation to the settlement level in and around the reserve (e.g., Fig. 3a, which essentially converges after five iterations). DPR_{sat} is a particularly good estimate of the equilibrium state when FNEPR in fished areas is low (not shown). When the final state is

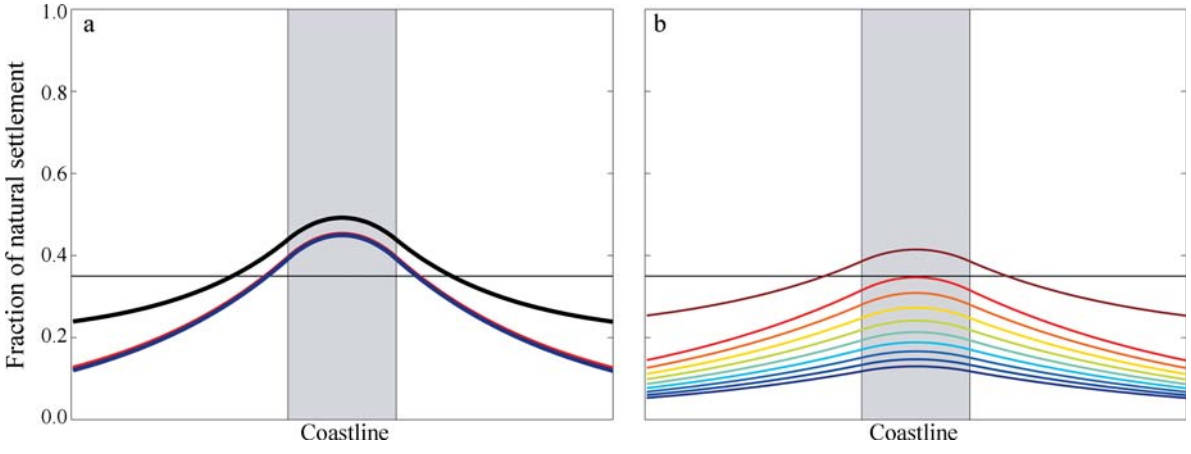

FIG. 3. Iterations of DPR_n for dispersal distances of (a) 1.1 and (b) 1.6 times the width of the reserve (shown in gray). Only every fifth DPR_n iteration is shown in (a) and (b). In total, 10 curves are shown in each panel. The first curve in both panels is DPR_{sat} and is identical in appearance to the corresponding curve in Fig. 2. In (a), DPR_n reaches the equilibrium settlement level in 5–10 iterations (the second and third curves), and therefore, some of the 10 curves cannot be seen as they are covered by higher iterations.

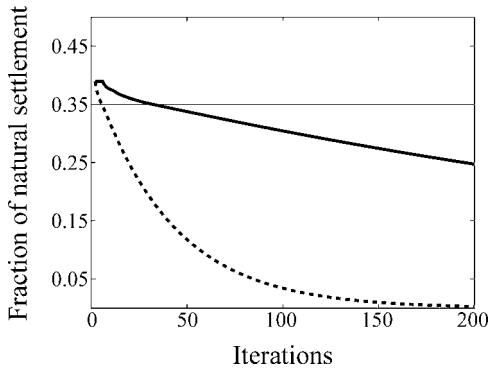

FIG. 4. Fraction of natural settlement at the center of the reserve for a full simulation of the population, including age structure (solid curve) and DPR_n (dashed curve), as a function of the number of iterations for a dispersal distance of 1.6 times the width of the reserve (i.e., the configuration shown in Fig. 3b). Note that DPR_n converges to the equilibrium value (zero in this case) far more rapidly than the full model.

collapse, convergence is slower, though often only a few iterations are needed to determine that settlement in all areas is less than f_{sat}, and that, therefore, collapse is inevitable (Fig. 3b). In all cases, this method of determining the equilibrium requires far fewer iterations than the full model (Fig. 4). The reason for this is that changes in settlement immediately produce changes in egg production in DPR_n because one always assumes that the population is at the stable age distribution. In the full model, changes in settlement only affect reproduction after recruits have become sexually mature, thereby requiring more time to reach equilibrium.

Persistence in uniform systems of reserves

Systems of marine reserves have been addressed by a number of authors (e.g., Botsford et al. 2001, Gaines et al. 2003). Here we focus on the utility of DPR for determining sustainability and yield. For uniform systems of reserves, we have extended the analytic expression for DPR_{sat} at the reserve edge in Botsford et al. (2001) to arbitrary locations and nonzero EPR in fished areas (see Appendix A).

The principal change in sustainability between an isolated reserve and a network of nearby reserves is the possibility of a "network effect." This network effect refers to when a population in a system of marine reserves persisted while the same population in an isolated reserve of the same size as one of the reserves in the network would collapse (Botsford et al. 2003). For example, the thick-solid black curve in Fig. 5a is for a dispersal distance of 1.1 times the reserve width, which persists for the system of reserves shown, but collapsed for a single isolated reserve (thick-solid red curve of Fig. 2a). Furthermore, if reserves cover a sufficiently large fraction of the coastline, the system will persist for arbitrarily large dispersal distances (Botsford et al.

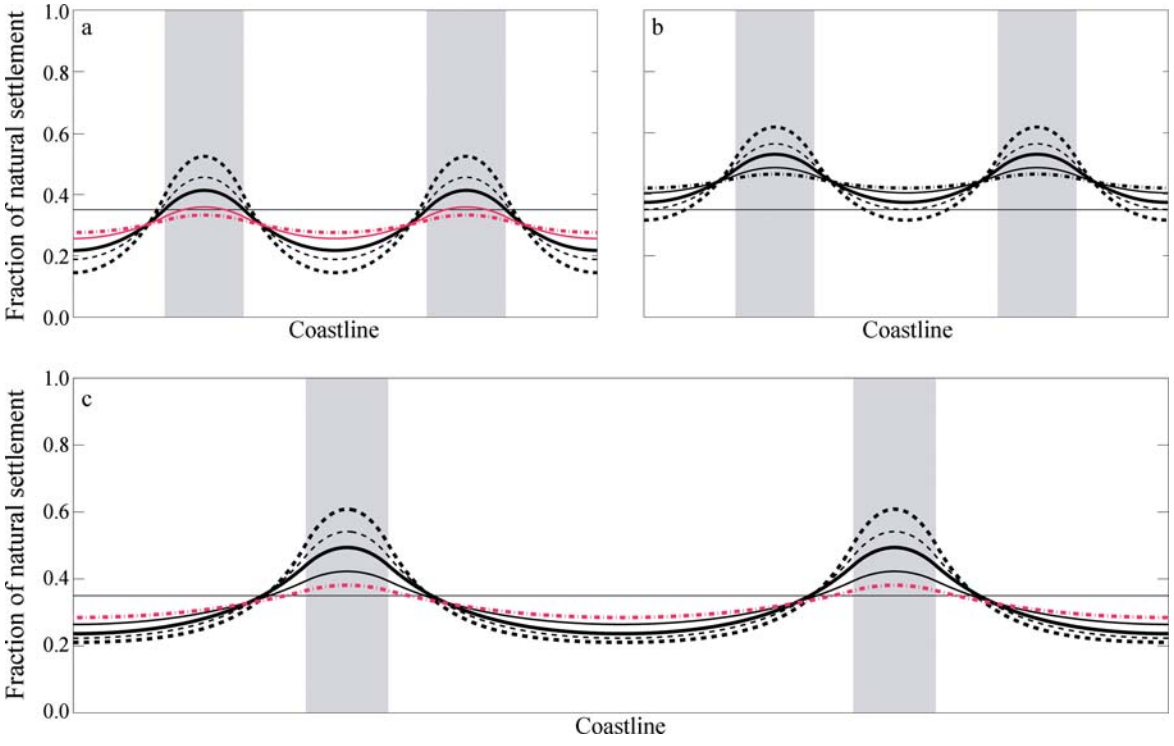

FIG. 5. DPR in systems of uniformly spaced, equal-sized marine reserves for several dispersal distances. Dispersal distances are the same as those in Fig. 2 (0.7, 0.9, 1.1, 1.6, and 2.2 times the width of a reserve). Reserves occupy 30% of the coastline in (a) and (b), and 15% in (c). FNEPR is 0.0 in (a), and 0.2 in (b) and (c). Red curves indicate populations that collapse.

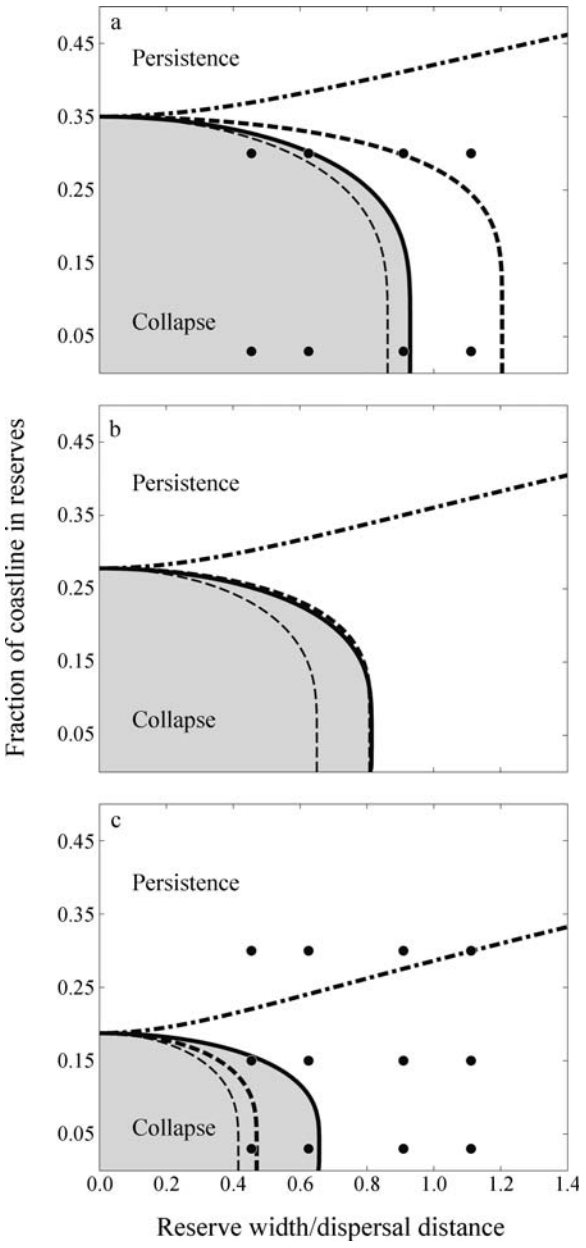

FIG. 6. Sustainability in uniform systems of marine reserves as a function of reserve width (in units of the dispersal distance) and the fraction of the coastline in reserves. FNEPR is 0.0, 0.1, and 0.2 in (a), (b), and (c), respectively. The solid curve indicates the border between the regions of persistence and collapse. Uniform reserve configurations above the dash-dotted curve have all locations saturated with recruits. Configurations above the thick dashed curve have DPR_{sat} greater than the saturation level in all reserve locations. Configurations below the thin dashed curve have DPR_{sat} less than the saturation level at all locations. The black dots in panels (a) and (c) indicate the reserve configurations shown in Figs. 2 and 3.

2001). If f_{sat} is uniform over space, the fraction of the coastline for which the population will persist for all dispersal distances can be determined from the requirement that the settlement rate at infinite dispersal distance (i.e., even distribution of larvae over all of space) must saturate the system with larvae:

$$P \cdot 1 + (1 - P) \cdot \text{FNEPR} > f_{sat} \tag{12}$$

where P is the fraction of the coastline in reserves. After rearranging the terms, one finds that the fraction of coastline in reserves must satisfy

$$P > \frac{f_{sat} - \text{FNEPR}}{1 - \text{FNEPR}} \tag{13}$$

to guarantee persistence for arbitrarily large dispersal distances.

DPR in systems of reserves has four possible outcomes: the three discussed previously ($DPR_{sat} < f_{sat}$ everywhere (not shown), $DPR_{sat} > f_{sat}$ in some reserve areas, and $DPR_{sat} > f_{sat}$ in all reserve areas), as well as $DPR_{sat} > f_{sat}$ everywhere. As before, collapse will occur if DPR_{sat} is less than f_{sat} everywhere. $DPR_{sat} > f_{sat}$ everywhere occurs when the fraction of the coastline in reserves and/or the FNEPR in fished areas are sufficiently high and the dispersal distance is sufficiently large so that both reserve and fished areas are habitat saturated (e.g., all but the thick-dashed curve in Fig. 5b). As all areas are saturated with larvae, persistence is guaranteed in this case, and DPR_{sat} gives the equilibrium settlement level.

The dependence of persistence in uniform systems of reserves on the fraction of the coastline in reserves and reserve width (in units of the dispersal distance) is shown in Fig. 6 (solid curve is the border of persistence region) for several values of FNEPR. So long as FNEPR in fished areas is less than f_{sat}, there is always a region of small reserve size and/or a small fraction of the coastline in reserves that produces population collapse (lower left of panels in Fig. 6). However, if the fraction of coastline in reserves is greater than the critical fraction in Eq. 13 (upper part of panels in Fig. 6) or individual reserves are sufficiently large (right-hand side of panels in Fig. 6), the population will persist (see also Botsford et al. 2001).

How the condition "$DPR_{sat} > f_{sat}$" in reserve areas relates to persistence depends on the FNEPR in fished areas. The three dashed curves in Fig. 6 indicate which of the four DPR_{sat} outcomes describes the system. Above and to the left of the dash-dotted curves shows $DPR_{sat} > f_{sat}$ everywhere, and persistence is guaranteed. This only occurs when more than the critical fraction of coastline is in reserves (i.e., Eq. 13 is satisfied). Below and to the left of the thin-dashed curves, DPR_{sat} is less than f_{sat} everywhere and collapse occurs. For the set of marine reserve configurations above and below these two curves, respectively, DPR_{sat} immediately determines the equilibrium state of the system regardless of FNEPR in fished areas. However, there are a large number of systems, including those configurations that are most likely to occur in real systems (small reserve size and small fraction of coastline in reserves), for which the relationship between DPR and persistence depends on the value of FNEPR in fished areas.

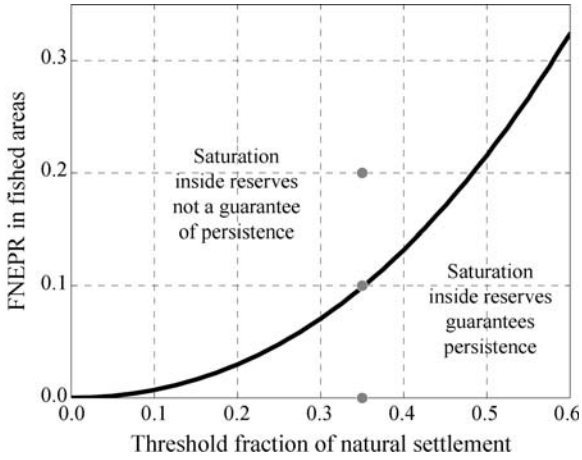

FIG. 7. The maximum FNEPR in fished areas for which saturation in all reserve areas for systems of uniformly spaced, equal-sized reserves ensures persistence as a function of the threshold fraction of natural settlement required for recruitment saturation (f_{sat}). The three gray dots indicate the levels of FNEPR and the threshold fractions shown in Fig. 4.

Marine reserve configurations above and to the right of the thick-dashed curves in Fig. 6 have $DPR_{sat} > f_{sat}$ in all reserve areas. For FNEPR = 0.0 (Fig. 6a), these configurations always persist. For FNEPR = 0.2, $DPR_{sat} > f_{sat}$ in all reserve areas is necessary for persistence but is not a guarantee of persistence. For FNEPR = 0.1, the persistence curve and DPR_{sat} above f_{sat} inside reserves curve nearly touch at small fractions of the coastline in reserves. In essence, this value of FNEPR is the largest value for which $DPR_{sat} > f_{sat}$ inside reserves is sufficient to guarantee persistence.

This last result is useful as it determines if persistence can be ascertained from DPR_{sat} alone, yet a more general result for arbitrary values of f_{sat} is desirable. The precise level of FNEPR less than which DPR_{sat} inside reserves greater than f_{sat} guarantees persistence can be determined as a function of f_{sat} by combining the analytic expression for DPR_{sat} at the reserve edge (Appendix A) with the expression for persistence in systems of uniform reserves contained in VanKirk and Lewis (1997) (see Appendix B for details). As f_{sat} is increased, this level of FNEPR increases as well, reaching ~0.2 when $f_{sat} = 0.5$ (Fig. 7).

Yield in uniform systems of reserves

Yield in systems of reserves can be determined using Eq. 10 from YPR in fished areas and the equilibrium levels of recruitment that result from the DPR_n calculations. For uniform systems of infinitely small marine reserves, yield is highest when reserves cover just enough of the coastline to guarantee persistence for all dispersal distances (Hastings and Botsford 2003). Maximum yields for finite reserve sizes occur when the density of reserves is such that nearly all areas are habitat saturated (Fig. 8; note proximity of dash-dotted

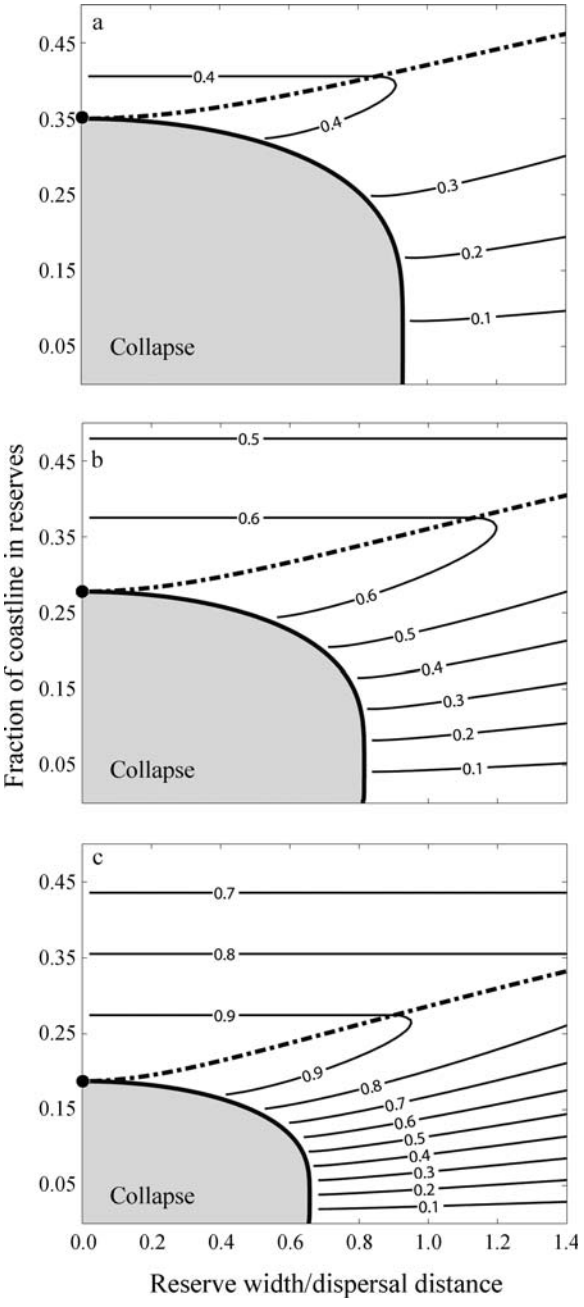

FIG. 8. Average yield per unit of habitat length for uniform systems reserves as a function of reserve width (in units of the dispersal distance) and fraction of the coastline in reserves. FNEPR is 0.0, 0.1, and 0.2 in (a), (b), and (c), respectively. Yield was calculated based on a von Bertalanffy growth function and cubic length to mass relationship. Values shown are relative to the maximum value for all three panels. The black dot along the left-hand edge of each panel indicates the reserve configuration with maximum yield for that level of FNEPR. The dash-dotted curves are as in Fig. 6.

curve and maximum yield for fixed reserve size and dispersal distance). If settlement is above the line indicating habitat saturation in all areas (configurations above the dash-dotted curve in Fig. 8), recruitment is

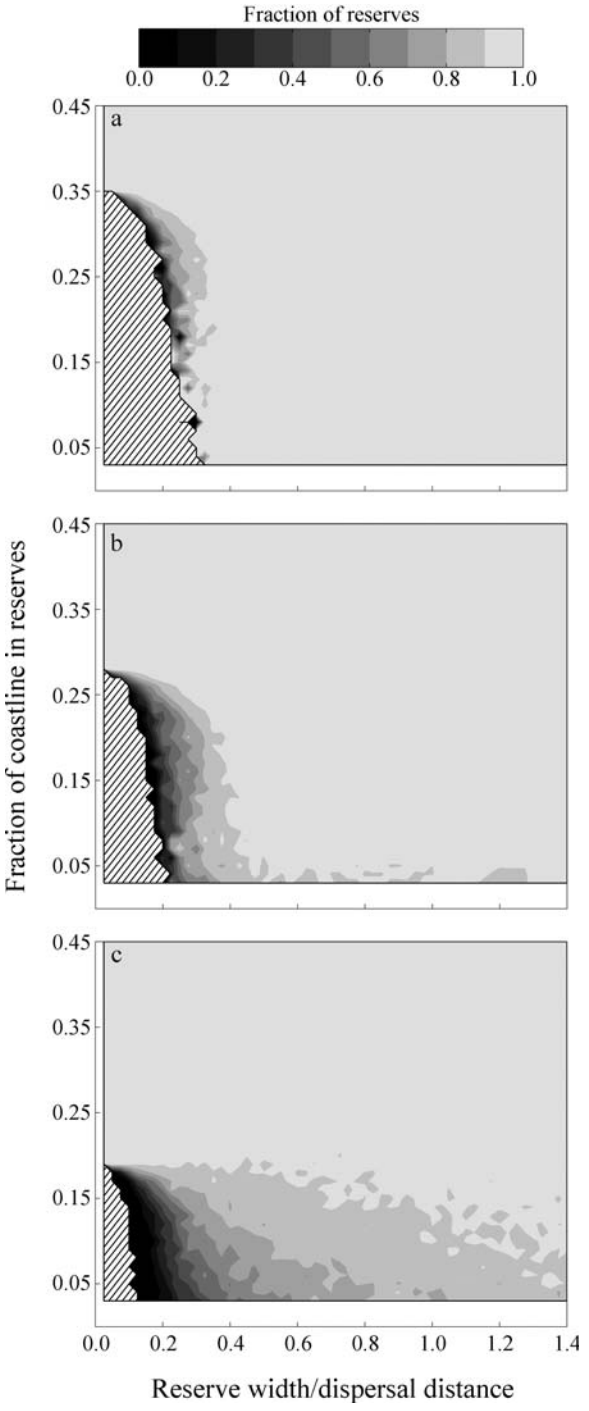

FIG. 9. Fraction of reserves for which $DPR_{sat} > f_{sat}$ throughout the reserve correctly indicates that the reserve is persistent (defined as equilibrium settlement greater than f_{sat} somewhere in the reserve). Reserves were randomly sized and spaced. FNEPR is 0.0, 0.1, and 0.2 in (a), (b), and (c), respectively. Hatched areas indicate that no reserves tested had $DPR_{sat} > f_{sat}$ throughout. Note that some of the apparent structure in the panels [particularly notable in (b)] is due to the underlying spatial discretization and would not be present in a truly continuous system.

constant over space, and total yield depends linearly on the fraction of coastline in reserves and is independent of reserve width: $Y = \mathrm{YPR} \cdot R_{sat}(1 - P)$, where P is the fraction of coastline in reserves. Surprisingly, yield is also relatively independent of reserve width when the fraction of coastline in reserves is small. In this case, yield increases approximately linearly with the fraction in reserves.

Persistence in systems of reserves with random size and spacing

While uniform systems of reserves are a useful example for exploring the possible effects of marine reserves on populations, real networks of marine reserves will have variability in the spacing between reserves and the size of reserves. It is difficult to analytically explore the utility of DPR for determining persistence and equilibrium population levels in all of these cases. Instead, we constructed many systems of randomly sized and spaced reserves and tested each reserve for persistence (defined as "DPR_{1000} greater than f_{sat} somewhere in the reserve"). This measure of true persistence was then compared with predictions of persistence based on DPR_{sat} being greater than f_{sat} in the reserve.

When there is variability in the size and spacing of reserves, persistence in an individual reserve depends on the size of the reserve and the proximity of other reserves. Mean reserve width and mean fraction of the coastline in reserves continue to be good indices of persistence, with roughly $\geq$50% of the reserves persistent when a uniform system of reserves with the same mean reserve width and coastline fraction would persist (Fig. C.1 in Appendix C).

$DPR_{sat} > f_{sat}$ in a reserve is an extremely good predictor of persistence when the FNEPR in fished areas is below the critical level shown in Fig. 7 (Fig. 9a, b). Except in exceptional cases where two or more small reserves are immediately adjacent to each other producing high levels of DPR_{sat} in one of the reserves but less than habitat saturation levels in the others, $DPR_{sat} > f_{sat}$ correctly predicts persistence nearly 100% of the time. Even when FNEPR is higher than the critical level in Fig. 7, DPR_{sat} above f_{sat} in the reserve is a good indicator of local persistence, though not an absolute guarantee (Fig. 9c). Furthermore, the majority of reserves that satisfy the habitat saturation condition but do not persist occur in systems whose fraction of coastline in reserves or mean reserve size is such that collapse would be expected in a uniform system of reserves with the same mean properties (compare Figs. 6c and 9c). The vast majority of reserves that are persistent also have DPR_{sat} above f_{sat} in the reserve (Fig. 10), indicating that the converse statement is generally true: if DPR_{sat} is less than f_{sat} somewhere in the reserve, the reserve population generally does not persist.

Use of DPR for the assessment of a realistic marine reserve configuration

Our results provide basic guidelines for determining the consequences of DPR_{sat} for predicting persistence in the population model we are using. Though these theoretical examples are extremely important for understanding DPR, the usefulness of DPR can be more fully appreciated by examining an example of its application to a realistic proposed system of reserves along a real coastline. Here we analyze one such example of a realistic marine reserve configuration based on available habitat and fisheries data for the central coast of California.

Two-dimensional habitat and reserve areas, as well as their one-dimensional representations, are shown in the first two panels of Fig. 11. Though the details of the offshore extensions of habitat and reserves are difficult to capture in one dimension, both are nearly one dimensional in this case due to the bathymetric limitations on habitat area; the one-dimensional representation of the system is an acceptable description of reserve size and spacing and of habitat availability (Fig. 11b).

As dispersal distances are typically uncertain and vary among species, several different distances were examined that ranged in size from somewhat shorter than most reserves (e.g., a dispersal distance of 1 km) to considerably larger than the average reserve (e.g., a dispersal distance of 25 km). The equilibrium state of the system (Fig. 11d) behaved as one would expect from the results of the previous sections, with persistence inside reserves for short-distance dispersers (e.g., black and blue curves of Fig. 11d) but with equilibrium settlement levels less than f_{sat} for longer dispersal distances in all areas except those with relatively large reserves or a high density of reserves (green and red curves; Fig. 11d).

In general, DPR_{sat} levels were a good predictor of overall persistence in individual reserves for a range of dispersal distances. As the FNEPR level outside of reserves was mostly 0.2 (except in non-habitat areas, where it was 0.0), DPR_{sat} above f_{sat} throughout a reserve does not guarantee persistence (see Fig. 7). Nonetheless, in almost all cases, satisfying this condition correctly indicates that the equilibrium settlement level will be above f_{sat} somewhere in the reserve (compare Fig. 11c, d). For short dispersal distances, DPR_{sat} levels are very close to the equilibrium settlement levels. For longer dispersal distances, DPR_{sat} only approximates equilibrium settlement in areas where the equilibrium settlement is high. However, these areas can be correctly identified from DPR_{sat} levels. For example, for a dispersal distance of 25 km (red curve), DPR_{sat} levels in Fig. 11c are just above f_{sat} throughout the reserves around kilometer 200, but are slightly less than f_{sat} in some parts of the reserves around kilometer 400. The resulting equilibrium settlement is above f_{sat} around kilometer 200, but less than f_{sat} around kilometer 400 (Fig. 11d).

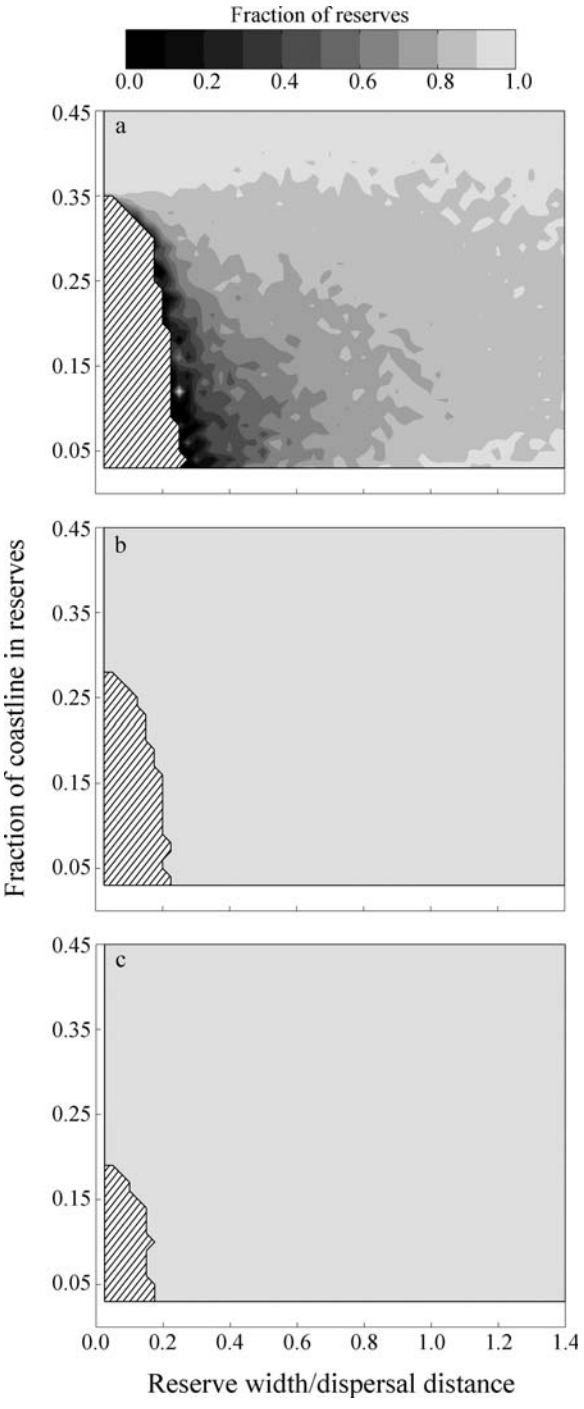

FIG. 10. Fraction of persistent reserves for which DPR_{sat} is greater than f_{sat} throughout the reserve (i.e., what fraction of the time persistence indicates that DPR_{sat} is greater than f_{sat} throughout the reserve). Reserves were randomly sized and spaced. FNEPR is 0.0, 0.1, and 0.2 in (a), (b), and (c), respectively. Hatched areas indicate that no reserves tested were persistent.

Discussion

We have developed a simple method for estimating spatial patterns of settlement and yield of a population with sedentary adults and dispersing larvae in a system of marine reserves. DPR greatly simplifies the problem of determining persistence in systems of marine reserves by eliminating the need to specify a full model for the population and reducing the system to just the essential elements: the effects of fishing on reproduction, the carrying capacity of post-settlement habitats and the connectivity between different locations through larval dispersal. These simplifications reduce the computer time necessary to determine population persistence in a marine reserve configuration and streamline the assessment of uncertainties in model parameters. Furthermore, DPR is simple enough that it can potentially be integrated into existing tools for spatial management (e.g., GIS-based tools).

From a theoretical population dynamics point of view, the DPR approach reduces the full model system to that of an equivalent semelparous population by integrating over the adult life phase. In essence, the effect of the adult population on the equilibrium state of the system is contained in the EPR level at each point in space. This reduced model system has the same equilibrium, but cannot be used to study the temporal evolution of the full model system. This approach is a numerical application of the replacement concept (e.g., Eq. 1), which contains information on whether the population is increasing, but not the rate at which it increases (similar to the difference between R_0 and λ; Caswell 2001). The replacement concept has been useful in a variety of applications, including fisheries, and here is extended to spatial management of marine populations. It is similar to but differs from other approaches to persistence of marine metapopulations (e.g., Armsworth 2002, Kritzer and Sale 2006). For example, a more analytical approach, which defines persistence as instability about the zero state, provides additional guidance regarding the characteristics that lead to persistent marine metapopulations (Hastings and Botsford 2006).

Through applications of DPR to marine reserve systems along linear coastlines, we have outlined a basic procedure for using DPR to evaluate designs of marine protected areas based on currently available fisheries and larval dispersal information. In those cases most relevant for the reserve systems currently being implemented (i.e., small fractions of the total habitat in reserves, small reserve widths and high fishing rates), there will likely be areas that receive insufficient settlers to assure habitat saturation, and DPR will not give the exact settlement level. However, if the FNEPR in fished areas is low (e.g., in our model, FNEPR < 0.1 for $f_{sat} = 0.35$), then local persistence is very likely if DPR_{sat} inside the entire reserve is greater than f_{sat}. In these cases, DPR_{sat} is an upper bound estimate of the equilibrium settlement level. This result applies to both uniform and nonuniform distributions of reserves. In cases where FNEPR in fished areas is relatively high, $DPR_{sat} > f_{sat}$ inside reserves is a prerequisite for persistence and a good indicator of the state of the system, but does not guarantee persistence. The precise level of FNEPR above which the condition DPR_{sat} greater than f_{sat} inside reserves is not a guarantee of persistence will depend on the dimensionality of the system, the form of the dispersal matrix, and the settler–recruit relationship, but the general procedure described here is unlikely to change.

In cases where DPR_{sat} does not provide sufficient information to determine the equilibrium state of the system and there are sufficient data to estimate a functional form for the settler–recruit relationship, DPR_n can be used to rapidly determine the true equilibrium settlement, recruitment, and yield. Speed improvements when using DPR_n relative to the speed of the full population model will be significant in populations for whom detailed stage or age structure is important, e.g., long-lived fish species whose reproductive output changes significantly over its lifetime. Furthermore, two-dimensional systems and systems with many subpopulations will also benefit significantly as they require large matrices to describe.

The ultimate success of decision-making processes that make use of DPR calculations will depend on the appropriate characterization of the various uncertainties in the outcomes. DPR can be evaluated for various marine reserve configurations, dispersal distances, fishing levels, and habitat saturation levels to assess how persistence is affected by each of these parameters. In particular, the habitat saturation level f_{sat} is typically highly uncertain. One of the primary advantages of the DPR_{sat} calculation is that it is independent of the habitat saturation level, and a single such calculation can be compared to multiple f_{sat} levels. This approach provides a logical means for making a comprehensive assessment of the effects of uncertainties in the model.

The DPR method combined with habitat distributions, reserve configurations, and fisheries data provides a framework for predicting the benefits to persistence from a marine reserve network. Once a particular marine reserve configuration has been implemented, DPR estimates of spatial patterns of settlement can be compared with long-term settlement observations to try to understand some of the uncertainties and assess the potential effects of mechanisms not included in the original model. Few data sets currently exist that would make such comparisons feasible, but this is likely to change as marine reserves are implemented and longer time series become available.

DPR is complementary to reserve-siting algorithms that efficiently choose the spatial configurations of reserves that include a desired mix of adult habitats and species (e.g., Leslie et al. 2003). Persistence is not normally addressed by siting algorithms alone, as they

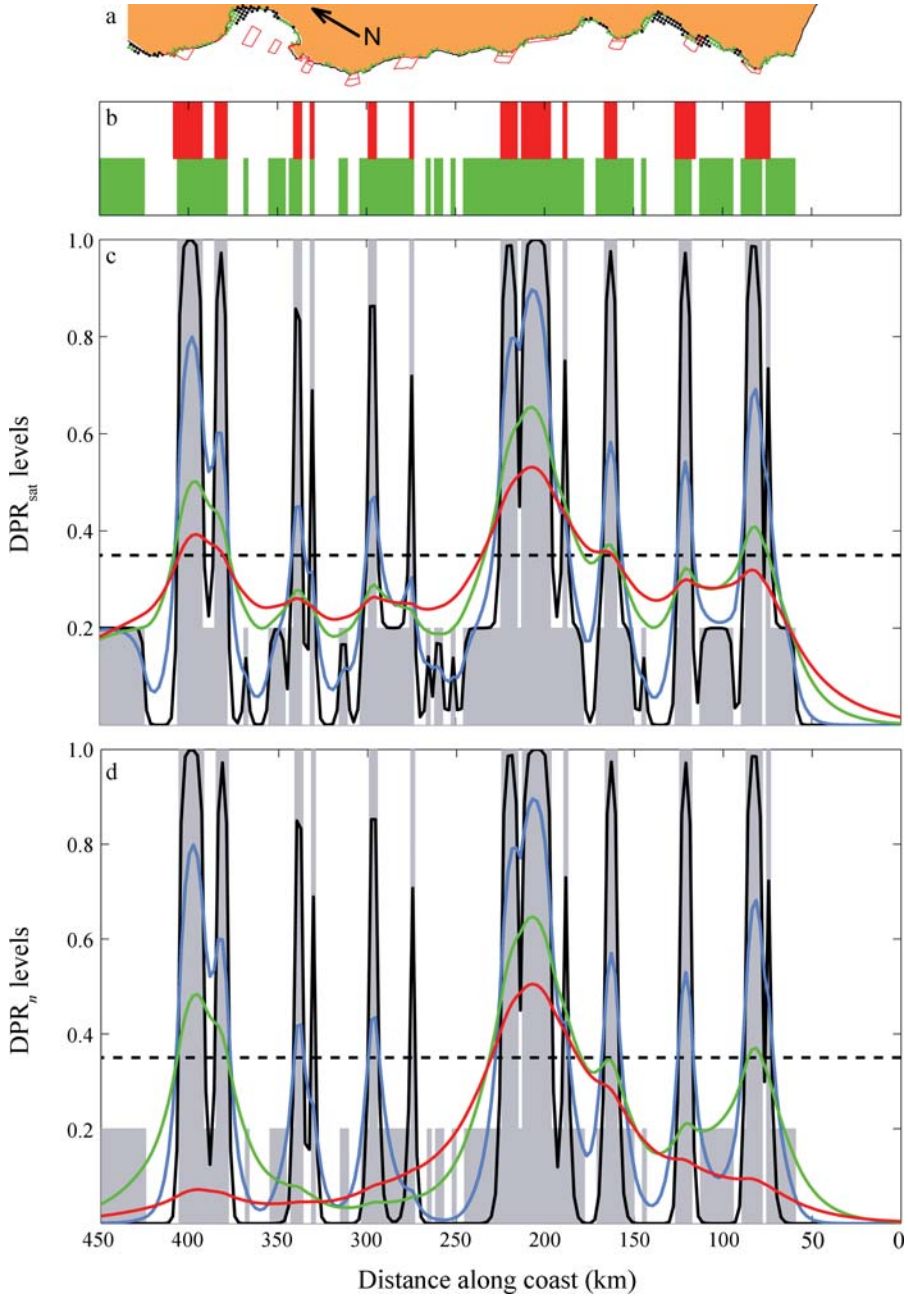

FIG. 11. Realistic marine reserve configuration assessed using the DPR method. (a) The coastline of central California with 0–30 m depth shows rocky-bottom habitat areas indicated by green dots, non-habitat areas indicated by black dots, and reserve areas outlined in red. In (b), the information in (a) is binned by latitude to yield a linear coastline with reserve areas (in red) and habitat areas (in green) that approximate the original two-dimensional system. (c) The resulting FNEPR levels (gray areas) and DPR_{sat} levels (curves) for dispersal distances of 1 km (black), 5 km (blue), 15 km (green), and 25 km (red). Similarly, the equilibrium settlement levels as estimated by DPR_{100} are shown in (d).

do not take into account the distribution of habitat areas between reserves and the connectivity between populations through larval dispersal. By combining siting-algorithm approaches with DPR, systems of marine reserves that efficiently incorporate key habitats and assure persistence of the populations in those habitats can, potentially, be created.

In addition to providing information on the performance of DPR computations, the analyses presented here improve our general understanding of yield in systems of marine reserves. Previous results showed that maximum yield from a system of reserves would occur with the smallest possible reserves that cover the minimum fraction of coastline required for persistence

(Hastings and Botsford 2003). Here we extend these results to reserves of finite size. For any given reserve size, the fraction of the coastline in reserves that produces the highest yield is that which nearly saturates all post-settlement habitat with recruits (Fig. 8). Yield decreases for fractions considerably greater and less than the fraction at which habitat saturation of all areas just barely occurs. Furthermore, for fixed, small fractions of the coastline in reserves, yield is relatively constant for a wide range of reserve sizes. This suggests that yield will be most sensitive to the fraction of coastline in reserves and relatively insensitive to the size of individual reserves. However, the robustness of this pattern to changes in the form of the dispersal pattern is not clear, and a non-uniform distribution of fishing effort could significantly affect these results (e.g., Smith and Wilen 2003, Halpern et al. 2004).

While DPR provides a tool for estimating population persistence in a wide variety of spatial management situations, there is considerable scope for further development. We have not considered net alongshore advection of larvae (but see, for example, Botsford et al. 2001, Gaines et al. 2003, Kaplan 2006), more complex forms for the settler–recruit function, or spatial variability in the suitability of habitats for the recruitment of settlers (i.e., variability in the level of f_{sat}). Though these factors will undoubtedly affect some of the conclusions in this paper, we suspect that our results will serve as a useful basis for understanding the behavior of these systems.

In conclusion, DPR is a generic tool for assessing persistence and yield in marine reserve networks. It has the advantages of being parsimonious and independent of a specific settler–recruit relationship. We have given a set of rules for interpreting the results of DPR analysis for persistence in a class of marine systems whose complexity and level of detail is commensurate with fisheries and habitat data that are currently available. These techniques are complementary to reserve-siting algorithms and could play an important role in the evaluation of proposed systems of marine reserves. In particular, using this approach requires that managers consider the ultimate consequences of marine reserves for population sustainability. These consequences might otherwise be ignored or inadequately addressed without such an approach.

Acknowledgments

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APPENDIX A

Analytic expression for DPR_{sat} in uniform systems of reserves (*Ecological Archives* A016-071-A1).

APPENDIX B

Maximum FNEPR in fished areas for which $DPR_{sat} > f_{sat}$ in all reserves areas guarantees persistence (*Ecological Archives* A016-071-A2).

APPENDIX C

A figure showing fraction of persistent reserves in randomly sized and spaced reserves on an infinite coastline (*Ecological Archives* A016-071-A3).