

Model-based assessment of persistence in proposed marine protected area designs

DAVID M. KAPLAN,^{1,7} LOUIS W. BOTSFORD,² MICHAEL R. O'FARRELL,³ STEVEN D. GAINES,^{4,5}
AND SALVADOR JORGENSEN⁶

¹*Institute of Marine Sciences, University of California, Santa Cruz, California 95064 USA*

²*Department of Wildlife, Fish and Conservation Biology, University of California, Davis, California 95616 USA*

³*National Oceanic and Atmospheric Administration, Fisheries Ecology Division, Southwest Fisheries Science Center,
110 Shaffer Road, Santa Cruz, California 94920-1211 USA*

⁴*Marine Science Institute, University of California, Santa Barbara, California 93106-6150 USA*

⁵*Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106-6150 USA*

⁶*Tuna Research and Conservation Center, Hopkins Marine Station of Stanford University, and Monterey Bay Aquarium,
120 Oceanview Boulevard, Pacific Grove, California 93950 USA*

Abstract. Assessment of marine protected areas (MPAs) requires the ability to quantify the effects of proposed MPA size and placement, habitat distribution, larval dispersal, and fishing on the persistence of protected populations. Here we describe a model-based approach to assessment of the contribution of a network of marine protected areas to the persistence of populations with a sedentary adult phase and a dispersing larval phase. The model integrates the effects of a patchy spatial distribution of habitat, the spatial scale of larval dispersal, and the level of fishing outside of reserves into a calculation of the spatial distribution of equilibrium settlement. We use the amount of coastline predicted to have equilibrium settlement rates that saturate post-settlement habitat as a response variable for the assessment and comparison of MPA network designs. We apply this model to a set of recently proposed MPA networks for the central coast of California, USA. Results show that the area of habitat set aside is a good predictor of the area over which population levels will be high for short-distance dispersers. However, persistence of longer distance dispersers depends critically on the spatial distribution of habitat and reserves, ranging from not persistent anywhere to persistent over a greater area than that set aside in reserves. These results depend on the mechanisms of persistence, with self-replacement supporting short-distance dispersers and network effects supporting long-distance dispersers. Persistence also depends critically on fishery status outside the MPAs, as well as how fishing effort is redistributed after MPA implementation. This assessment method provides important benchmarks, as well as a transparent modeling approach, for improving initial MPA configurations that may result from less-comprehensive rule- or habitat-based methods of designing MPAs.

Key words: California coastline, USA; fisheries management; fishing; habitat distributions; larval dispersal; marine conservation; marine protected areas; metapopulations; modeling; persistence; rockfish; *Sebastes* spp.

INTRODUCTION

The goals of marine protected areas (MPAs) typically include biodiversity protection or an improvement in the status of economically important fish stocks. Both of these general MPA goals require the sustainability or persistence of populations in and around MPAs, yet persistence is often not evaluated. Rather, it is assumed that if patches of habitat are protected, species will persist in them. This “habitat-based” approach to the design and assessment of MPA networks seeks to

efficiently choose reserve sites with a specified fraction of existing habitats, species, or adult fish (e.g., Sala et al. 2002, Airame et al. 2003, Gladstone 2007, Lombard et al. 2007), primarily through the use of optimal siting algorithms, such as MARXAN (Ball and Possingham 2000, Possingham et al. 2000). However, as most marine populations reproduce through a dispersing larval stage, persistence of populations will depend on the connectivity among subpopulations through larval dispersal, in addition to the distribution of habitats and the population status in and around the MPAs. Thus, the presence of species in specific habitat areas cannot be assured by habitat-based choices alone, and assessing the sustainability of populations requires a population model that incorporates these factors.

In this paper, we apply a model of the dynamics of a marine population with sedentary adults and dispersing

Manuscript received 15 October 2007; revised 28 April 2008; accepted 20 June 2008. Corresponding Editor: S. S. Heppell.

⁷Present address: Centre de Recherche Halieutique Méditerranéenne et Tropicale, Institut de Recherche pour le Développement, Av. Jean Monnet, B.P. 171, 34203 Sète Cedex, France. E-mail: David.Kaplan@ird.fr

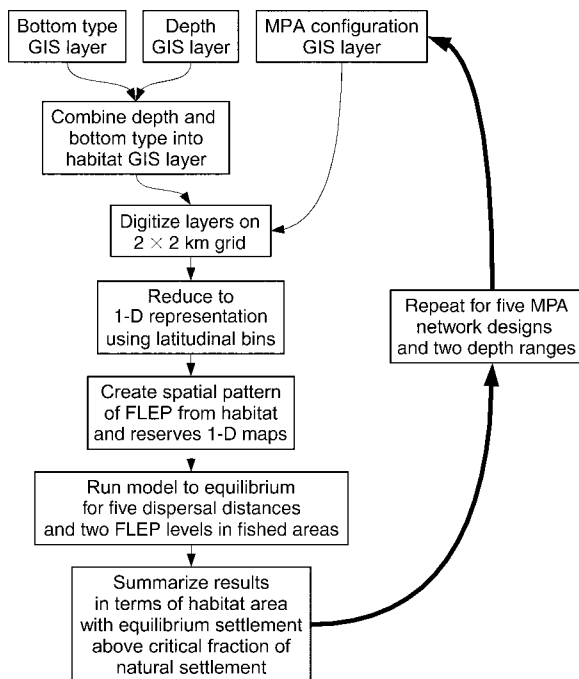


FIG. 1. Conceptual flow chart of methodology used to evaluate persistence in marine protected area (MPA) designs. Other abbreviations are: GIS, geographic information system; FLEP, fraction of lifetime egg production.

larvae (Kaplan et al. 2006) to the practical problem of the assessment of persistence for various species in proposed networks of MPAs. Our approach integrates the spatial distribution of habitat, the spatial scale of larval dispersal, and the level of fishing outside of reserves into a quantitative prediction of the spatial pattern of population persistence that will result from proposed MPAs. This approach is complementary to habitat-based approaches as it adds a direct evaluation of persistence. We use the example of five proposed MPA networks for the central coast of California as a demonstration of the use of such a model to provide scientific support for decision-making in MPA implementation.

This study represents a shift in emphasis from most previous model-based evaluations of MPA effects, which have principally focused on the general question of when MPAs provide for globally persistent populations (e.g., as in Botsford et al. 2001). In the context of MPA design and assessment, one is interested not just in providing a hedge against extinction (i.e., global persistence, there being at least one population somewhere), but also in assuring that species are represented in significant numbers at specific locations and over the majority of their natural ranges. A widely distributed population is desirable from ecological (e.g., providing redundancy as protection against local environmental variability, disturbance, or climate change; Allison et al. 2003), evolutionary (e.g., maintenance of genetic diver-

sity; Bell and Okamura 2005), and fisheries (e.g., to provide a large area with high yields) points of view. This local definition of the words “sustainable” and “persistent” will be the focus here; examples of other modeling studies that have a similar vision were conducted by Mahevas and Pelletier (2003), Meester et al. (2004), and Walters et al. (2007). Specifically, we will be assessing the length of coastline over which a species receives sufficient new settlers to maintain high local recruitment levels. We use the length of coastline with high recruitment rates as an indicator of the local “health” or “persistence” of the population. Despite this shift in focus from global to local persistence, we find it useful to interpret our assessments in terms of earlier, more general results, and our results provide insight into the likely differences between more idealized assessments of MPA effects and the practical assessments addressed here.

A second shift in emphasis is that we explicitly account for actual spatial structure of the habitat in our assessments, rather than assuming constant habitat, as was frequently done in previous modeling studies (e.g., Botsford et al. 2001). This improves estimates of species distributions at the cost of obtaining maps of marine habitats at spatial scales appropriate for capturing habitat patchiness. Here we demonstrate our approach with hard-bottom species (i.e., rockfish on rocky reefs), but a complete assessment would repeat the analysis with maps of other relevant habitat types (e.g., sand bottom areas for flatfish assessment).

Our goals here include providing a detailed description of our modeling approach so that others may use this approach to integrate realistic patterns of habitat and reserves for other similar MPA assessments. We further demonstrate the utility of this model by comparing improvements in persistence provided by each of the five California MPA proposals and show how results obtained can be explained in terms of previous MPA analyses. We place this comprehensive model-based approach in the context of less comprehensive rule- or habitat-based MPA design systems and describe how the various approaches can be integrated. Finally, we note the consequences of some of the underlying assumptions and uncertainties in our modeling approach with an eye toward future improvements and extensions.

MODEL DEVELOPMENT

An overview of our entire modeling process is conceptually illustrated in Fig. 1. The model used in this study is the dispersal-per-recruit (DPR) model described in Kaplan et al. (2006; specifically the iterative approach in that study). This model describes the dynamics of an age- or stage-structured, spatially distributed marine metapopulation with dispersing larvae and sedentary adults. Though the model itself is not limited to a single spatial dimension, we will use a linear coastline here. Recruitment of new individuals to

the adult population at each location is governed by a density-dependent relationship that depends upon the number of settlers (i.e., individuals that are competent for recruitment, but have not yet entered the adult population) arriving at that location. This local density-dependent relationship is the spatial analogue of the stock–recruitment relationship used in many nonspatial fisheries stock assessments (e.g., Myers et al. 1999). Here we use a deterministic, nondecreasing function, representing a limited capacity of the post-settlement environment, which becomes saturated at high settlement.

The DPR modeling approach uses lifetime egg production (LEP) to represent the effects of fishing on a fish population. Lifetime egg production is the number of eggs that an average recruit produces over its lifetime. This quantity summarizes the effects of survival and reproduction on the lifetime reproductive output of a typical individual in the population. Fishing reduces LEP by decreasing the average lifespan of an individual, thereby reducing the number of eggs an individual produces over its lifetime.

It has long been recognized that LEP is a measure of individual replacement (i.e., the ability of an individual to replace itself in the population via reproduction), hence it quantifies the inherent tendency of a population to persist (e.g., Caswell 2001 for linear models). In a nonspatial context, it has been shown that a population with age structure and density-dependent recruitment will collapse if LEP is less than $1/s_0$, where s_0 is the slope at the origin of the density-dependent relationship between egg production and recruitment (i.e., the stock–recruitment relationship; Shepherd 1982, Sissenwine and Shepherd 1987, Botsford 1997). Because of this, LEP or similar concepts, such as spawning stock biomass per recruit (SSB/R), spawning potential ratio (SPR), and eggs per recruit (EPR), have been used in fisheries management to represent the effects of fishing on population persistence (e.g., Goodyear 1993, Mace and Sissenwine 1993, O’Farrell and Botsford 2005). Where information on egg production and recruitment at low abundance are available, it has been possible to estimate s_0 and thus establish the lower limit on LEP, below which a population will collapse (e.g., Mace and Sissenwine 1993, Myers et al. 1999). In an attempt to establish consistency across species so that species for which there is no data at low abundance can be managed, fishery ecologists have assumed that this threshold value of LEP is a certain fraction of the unfished value of LEP for each species (e.g., Mace and Sissenwine 1993). We refer to this as the fraction of lifetime egg production (FLEP). Based on meta-analyses of stock assessments for a wide variety of species and other factors, fishery ecologists have chosen precautionary values for FLEP of 35% and higher as management targets (e.g., Mace and Sissenwine 1993, Clark 2002), though actual thresholds may be lower.

The utility of LEP for describing the persistence of marine metapopulations in the context of MPAs was described in Botsford et al. (2001). Essentially, persistence in spatially distributed populations still depends on individual replacement through reproduction, but larval dispersal provides many more paths for replacement (see also Hastings and Botsford 2006). In the DPR model used here, Kaplan et al. (2006) showed how LEP enters the expression for the equilibrium spatial pattern of recruitment of age- or stage-structured marine metapopulations

$$\begin{aligned} S(x) &= \int D(x, y) \times \text{LEP}(y) \times R(y) d^m y \\ R(x) &= g[x, S(x)] \end{aligned} \quad (1)$$

where $S(x)$ is the number of settlers arriving at location x , $D(x, y)$ is the probability density that eggs produced at y settle at x , $\text{LEP}(x)$ is the spatial pattern of LEP, $R(x)$ is the number of recruits, and $g(x, S(x))$ is the density-dependent relationship between settlers and recruits at x . If it is assumed that the settler–recruit relationship is the same at all locations, then these equations can be rewritten

$$\begin{aligned} \hat{S}(x) &= \int D(x, y) \times \text{FLEP}(y) \times \hat{R}(y) d^m y \\ \hat{R}(x) &= \hat{g}[\hat{S}(x)] \end{aligned} \quad (2)$$

where FLEP is the fraction of natural LEP described above, $S(x)$ and $\hat{R}(x)$ are the settlement and recruitment, respectively, expressed relative to what one would have for a single, isolated population, and $\hat{g}(\hat{S})$ is the single, universal settler–recruit relationship. Kaplan et al. (2006) developed an iterative approach to solving these equations that consists of dispersing larvae from each point in space, initially assuming recruitment is at a level that saturates all post-settlement habitat areas and then summing the resulting larval settlement at each point to determine the recruitment level to be used in the next iteration.

The advantages to using this FLEP-based model are twofold. One is that we do not have to describe the specific juvenile and adult life histories of the species of interest, but rather can use FLEP to measure the effects of adults on population persistence. The equilibrium level of settlers and recruits obtained from the equations above is identical to what would be found with a full age- or stage-structured model. One can, therefore, examine the dynamics of a wide class of adult population life histories by just considering different spatial patterns of FLEP, without making reference to the particular life-history traits and fishing levels that produce the FLEP pattern. Second, the iterative approach to solving Eq. 2 converges much faster than a full age-structured simulation for long-lived species, thereby considerably reducing the computational time necessary to examine a wide variety of MPA configurations and FLEP patterns.

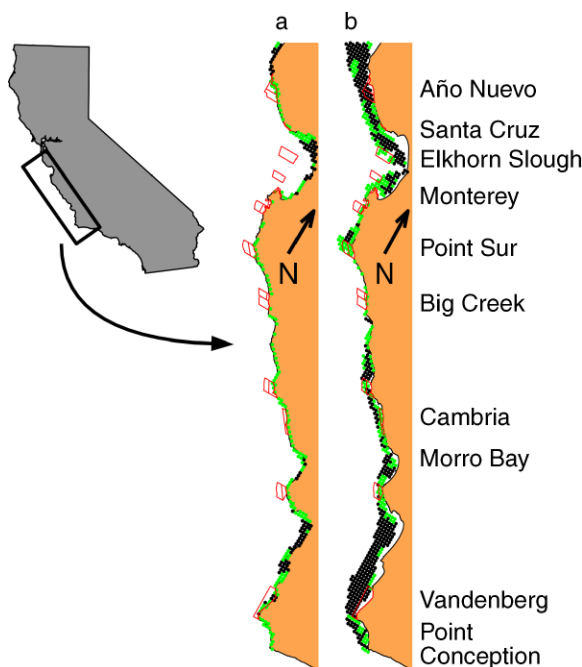


FIG. 2. Gridded two-dimensional habitat maps for (a) 0–30 m depth hard-bottom habitat and (b) 30–100 m depth hard-bottom habitat along the central coast of California, USA. Red lines indicate the borders of the final marine protected area (MPA) network selected by the California Fish and Game Commission. Green dots indicate habitat areas, black dots indicate non-habitat areas. A map of California with a box indicating the study area is to the left of the panels, while names of well-known locations along the central coast of California (that are also used in Fig. 3) are to the right of the panel. Note that for simplicity the extensive habitat buffer area to the north of the central California coast study area is not shown in either panel.

While this paper focuses on practical assessments of proposed MPAs, previous modeling studies of idealized MPA systems provide some basis for expectations regarding how MPAs affect population persistence for various values of FLEP. For example, for an infinite coastline, symmetric dispersal, and periodic MPAs with no larval contributions from fished areas, population persistence fell into two categories: (1) individual MPAs sustained populations with mean dispersal distances on the order of the dimension of the MPA or less and (2) multiple MPAs sustained populations regardless of dispersal distance when the fraction of coastline in MPAs exceeds the minimum value of FLEP required for population persistence (Botsford et al. 2001). The former was due to self-replacement because sufficient larvae return to settle in the same MPA, and the latter was termed a network effect because replacement occurred through a number of MPAs acting together (Hastings and Botsford 2006). Subsequent analyses showed how lower fishing mortalities than originally assumed led to greater persistence and that an advective

component in larval dispersal reduced persistence (Botsford et al. 2001, Kaplan 2006, Kaplan et al. 2006).

Application of DPR model to California MPA proposals

From Eq. 2, we can see that the application of the DPR approach to the assessment of proposed MPA designs requires assembling available data to determine the spatial distribution of FLEP. The FLEP levels reflect the effects of fishing on the population; hence they depend on the pattern of MPAs and management of fisheries outside the MPAs, including any shift in fishing effort with the implementation of MPAs. They also depend on whether a species can inhabit a location, hence on the spatial distribution of habitat.

The development of the assessments begins with spatial maps of habitat and marine reserves (Fig. 2). For the California MPA networks, water depth, bottom type, and marine reserve geographic information system (GIS) layers were obtained from the California Department of Fish and Game (DFG; *available online*).⁸ Depth and bottom type layers were assembled by the DFG based on a variety of existing data sets. Because the spatial resolution and quality of these data sets varied, the accuracy of the habitat maps derived from these layers also varied, with a tendency toward lower quality toward the southern end of the study region. Nonetheless, these maps represent the best available representations of fish habitat in the region.

We assessed five different proposed systems of MPAs (Fig. 3; three proposals made by stakeholders [1, 2R, and 3R]; a configuration proposed by the Department of Fish and Game [P]; and the final configuration implemented by the Fish and Game Commission [Comm]). Some MPAs were strictly no-take areas, while others allowed for some recreational and/or commercial fishing activity. The model was run for two versions of these MPA networks, one including only the no-take areas (the dark gray areas in Fig. 3) and the other including all MPA regardless of their level of protection (both the dark and light gray areas in Fig. 3).

We consider two habitat types here: hard-bottom, shallow-water habitat (0–30 m depth; Fig. 2a) and hard-bottom, deeper-water habitat (30–100 m depth; Fig. 2b). The first of these habitats can be thought of as kelp forest habitat, while the latter represents mid-shelf rocky-bottom areas. Both are host to a variety of species that are of great interest to the MPA implementation process in central California, including a number of overfished rockfish species (O'Farrell and Botsford 2006).

Habitat and reserve locations were digitized on a 2×2 km grid oriented along latitude/longitude lines. Each grid point was declared to be part of one of the habitats and/or reserve areas if the center of the grid point fell inside the respective area. Because this part of the California coastline is approximately linear, these 2-D

⁸ (<http://www.dfg.ca.gov/biogeodata/gis/>)

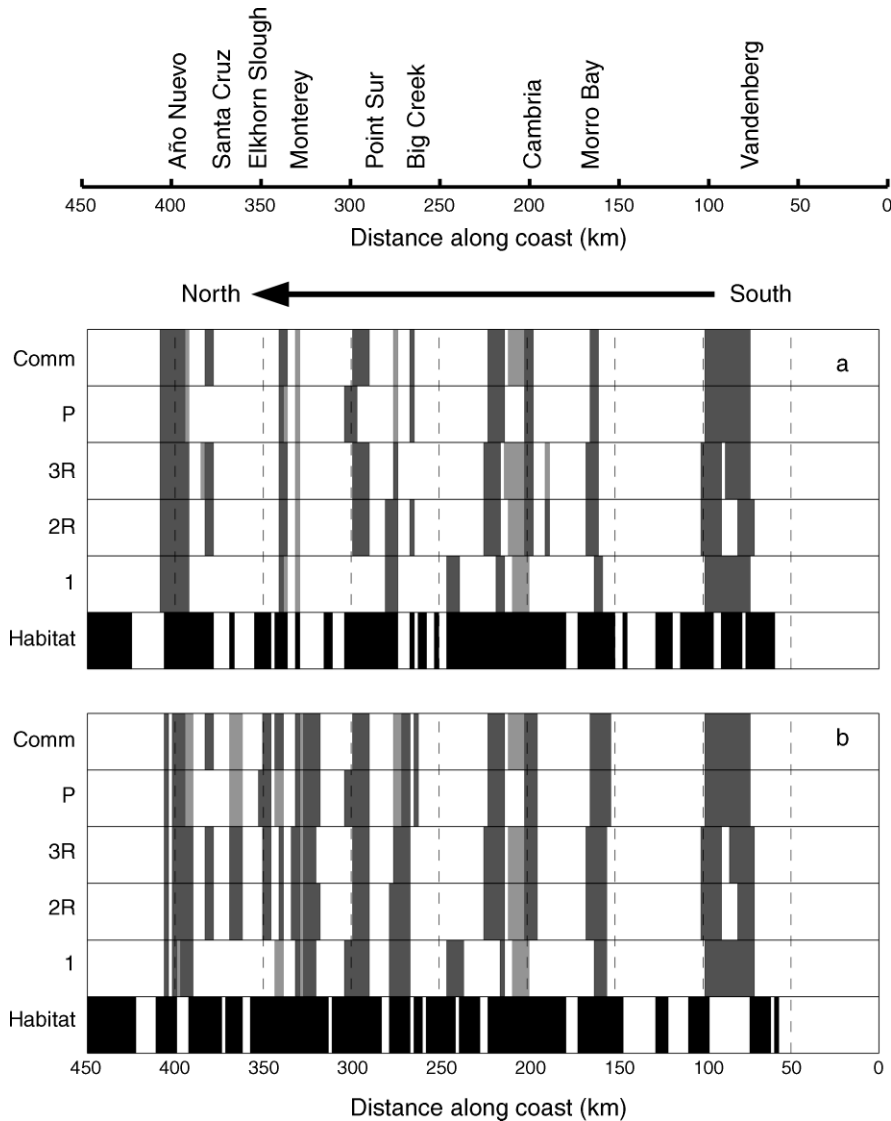


FIG. 3. One-dimensional representations of habitat (black) and reserve locations (dark gray and light gray; Comm, P, 3R, 2R, 1) in: (a) 0–30 m depth hard-bottom habitat and (b) 30–100 m depth hard-bottom habitat. Light gray areas indicate reserve areas that were classified by the science advisory team to the California Marine Life Protection Act implementation process as providing a lower level of protection than dark gray areas. See Table 2 for an explanation of the proposed marine protected area networks abbreviations. Note that for simplicity the extensive habitat buffer area to the north of the central California coast study area is not shown in either panel.

maps of habitat and reserve areas could be converted into 1-D representations in a straightforward manner. Grid points were grouped into 2 km wide latitudinal bins (~2.3 km wide in the alongshore direction, which is approximately 30° west of north in this region). If any grid point inside a latitudinal bin was in one of the habitat types or was a reserve area, then the entire latitudinal bin was considered to be that type. This reduction to 1-D produces a reasonable representation of the habitat and reserve areas and has the advantages of being simpler computationally because it avoids having to consider the full details of 2-D dispersal. This approximation has the disadvantages that in areas where

the shelf is unusually wide it underestimates the total habitat, while in areas where the shelf is very narrow it tends to overestimate or not capture habitat areas because of the 2-km grid resolution. Furthermore, some proposed MPA configurations contained very narrow reserves that did not cover the full offshore extent of habitat, resulting in exaggerated coverage by reserves in the 1-D representation. Despite these limitations, the 1-D representation of habitat and reserves captured the essential spatial variability in the factors affecting population persistence.

To account for the fact that habitat does not end at the boundary of the region, the 1-D representation of

TABLE 1. Fraction of total linear area in habitat with and without "buffer areas."

Hard-bottom habitat depth (m)	With buffers	Without buffers
0–30	0.60	0.68
30–100	0.66	0.73
0–100	0.81	0.86

Notes: Buffer areas are areas to the north and south of the central California coast, USA, study region where no reserves were proposed. These areas were included in the model runs to avoid unnatural edge effects but have been separated out here because the fraction in habitat in the study region is most relevant for the dynamics of the system. For comparison, we also include the fractions in habitat for 0–100 m hard-bottom habitat even though that habitat type is not included in our analyses.

the coastline was extended 200 km to the north of the central California region using available habitat maps. The 1-D habitat was extended to the south by only 50 km of non-habitat areas based on the fact that alongshore flows are predominantly equatorward and offshore in the vicinity of Point Conception, and, therefore, larvae produced south of the point have a low probability of being transported to habitat areas north of the point, producing a significant biogeographical barrier at the point (Wares et al. 2000, Gaines et al. 2008). While there is undoubtedly some level of larval transport from south of the point to the north, the approximation of zero connectivity would likely hold for the preponderance of species.

Each of the 1-D representations of habitat and reserves (Fig. 3) was then transformed into a spatial pattern of FLEP. In non-habitat areas, FLEP was assumed to be zero. For habitat areas inside reserves, a FLEP of 1.0 (i.e., the unfished LEP) was used. We considered two pre-reserve levels of FLEP in habitat areas that roughly cover the range of values for overfished rockfish in O'Farrell and Botsford (2006): 0.2 and 0.3.

The implementation of MPAs will likely lead to a redistribution of fishing effort, according to the new spatial restrictions and fishermen's anticipated revenues and costs (e.g., Smith and Wilen 2003). We did not model decision making by fishermen explicitly, but rather evaluated the effects of two different assumptions about the redistribution of fishing effort after the implementation of reserves. In the first, fishing effort is removed from the fishery by reserves so that pre- and post-reserve implementation FLEP values in non-reserve habitat areas are the same (i.e., 0.2 or 0.3). In the second, we maintained total fishing effort the same before and after MPA implementation by evenly redistributing effort that was previously in areas that become reserves into the remaining non-reserve habitat areas, thereby decreasing the FLEP values in non-reserve habitat areas (excluding the buffer zones, where FLEP continued to be 0.2 or 0.3). This redistribution is based on the fraction of the total area in habitat (Table 1) and reserves (Table 2), converting fishing rate to FLEP using life-history

TABLE 2. Fraction of one-dimensional central California coast habitat areas that is in reserve areas for the five proposed marine protected area (MPA) networks.

Proposed MPA network	All areas, 0–100 m	Hard bottom	
		0–30 m	30–100 m
1	0.31	0.27	0.24
2R	0.37	0.34	0.35
3R	0.37	0.35	0.34
P	0.34	0.26	0.32
Comm	0.36	0.32	0.34

Notes: Of the five proposed networks, 1, 2R, and 3R were proposed by stakeholder groups (naming does not represent any particular ordering), P is the plan recommended by the state Department of Fish and Game, and Comm is the final plan adopted by the state Fish and Game Commission. Fractions are calculated excluding buffer areas (areas outside of the central California study region that were included in the model for completeness but do not contain proposed reserves) and include all reserve areas without regard to presumed level of protection provided by the reserve (i.e., no-take reserves and reserves areas that allow some types of fishing).

information for black rockfish (O'Farrell and Botsford 2006). Though results may differ for other species, similarities in life-history traits suggest that the functional dependence of FLEP on fishing rate for black rockfish is representative of a variety of rockfish species in California waters (Love et al. 2002). The FLEP values after effort redistribution are shown in Table 3. We assume no spillover of adult fish from reserves into fished areas. Adult mobility, if present, could support some of this effort concentration, but would also reduce FLEP within reserves (Kellner et al. 2007).

A simple hockey-stick function was used to describe the relationship between the number of settlers arriving at a location and the final number of new recruits at that location (Barrowman and Myers 2000). In this relationship, as the number of settlers increases from zero, the

TABLE 3. Post-reserve-implementation fraction of lifetime egg production (FLEP) values in non-reserve habitat areas for five proposed marine protected area (MPA) networks, assuming that total effort remains the same as before MPA creation.

Pre-reserve FLEP value, by depth	Proposed MPA network				
	1	2R	3R	P	Comm
0–30 m hard bottom					
0.2	0.12	0.10	0.09	0.12	0.10
0.3	0.20	0.17	0.17	0.20	0.18
30–100 m hard bottom					
0.2	0.13	0.09	0.10	0.10	0.10
0.3	0.24	0.35	0.34	0.32	0.34

Notes: Of the five proposed networks, 1, 2R, and 3R were proposed by stakeholder groups (naming does not represent any particular ordering), P is the plan recommended by the state Department of Fish and Game, and Comm is the final plan adopted by the state Fish and Game Commission. All reserve areas regardless of protection level were included when calculating the results, though equivalent results were also obtained when only reserve areas classified as having a high level of protection were included (not shown).

number of recruits increases linearly until reaching a maximum carrying capacity. This relationship depends on the values of two parameters, the initial slope and the carrying capacity. These parameters were chosen so that a single, isolated population with this settler-recruit relationship would collapse at a FLEP of 0.35. This threshold value of FLEP was chosen not because we defend it as *the* value for the species of interest, but rather because it is an often-used reference point for the management of marine resources. A threshold value of 0.35 or greater is supported for three species of rockfish in a recent comprehensive estimate of slopes of egg–recruit relationships at low abundance (Myers et al. 1999; though one was an Atlantic species and the other two inhabit waters less than 100 m depth only as juveniles). Nevertheless, a value of 0.35 may be too high for some species and too low for others. Use of this specific value is not essential to our modeling approach, and a different value could be used. Furthermore, raising and lowering the FLEP threshold is roughly the equivalent of lowering and raising, respectively, the FLEP value in fished areas while holding the FLEP threshold value constant. Here we explore several different FLEP values in fished areas (including FLEP values from conservation of total fishing effort).

Information regarding larval dispersal patterns is extremely limited, typically consisting solely of an estimate of pelagic larval duration (Shanks et al. 2003). Information from genetic studies (e.g., Kinlan and Gaines 2003, Kinlan et al. 2005) and observations of elemental fingerprints (e.g., Miller and Shanks 2006) indicate there is a range of dispersal distances, but little detailed information on the shape of dispersal patterns and the level of alongshore advection is available. Given this level of information, we used an idealized dispersal pattern that is greatest at the point of larval production and decreases exponentially with linear distance from that point (i.e., a Laplacian distribution). This choice allows us to examine the effect of differences in dispersal distance without making unjustified assumptions regarding the form of the larval dispersal pattern. Population persistence is insensitive to the shape of the dispersal pattern (Lockwood et al. 2002), as long as it does not involve advection (Kaplan 2006). Nevertheless, integrating more realistic dispersal patterns that include spatial heterogeneity and alongshore advection is an important direction for future research (see *Discussion*).

Once parameterized for a given MPA configuration and set of assumptions about larval dispersal and fishing effort, the model was run through 300 iterations to produce an equilibrium spatial pattern of settlement. Results were summarized in terms of the fraction of the total habitat area that received sufficient settlers to saturate post-settlement habitat (i.e., areas where settlement was >35% of the unfished level for a single isolated population and, therefore, the highest possible recruitment level occurred at those locations). This is the area that we considered to be “persistent” in accordance

with the definition of persistence described in the *Introduction*. All fractions were calculated excluding the buffer areas to the north and south of the central California region where MPAs were being evaluated.

RESULTS

The DPR model was first applied to the 1-D representation of the central California system in the absence of MPAs with a variety of FLEP values in habitat areas and dispersal distances with the goal of understanding the effect of patchy habitat on persistence. The proposed MPA plans were then added to the system and spatial patterns of persistence were determined for each configuration.

Application of the model to the system in absence of reserves

Though the model has been configured so that a single isolated population with 100% self-recruitment will collapse when FLEP is below 0.35, the system representing the central coast of California differs from a single isolated population in several critical respects: (1) habitat is neither continuously nor evenly distributed in space, (2) as a result, recruitment at a location will depend on the spatial scale of larval dispersal, and (3) there is loss of larvae from the system at the edges. To determine the effect of habitat distribution on persistence as fishing effort is increased, we examined the model system for a variety of FLEP values in habitat areas and larval dispersal distances in the absence of marine reserves. We present here an example with no fishing for the two habitats (Fig. 4a, b) and an example in which fishing has reduced FLEP to 0.5 (Fig. 4c, d). Other examples with FLEP values between 0.4 and 1.0 can be found in Fig. A1 in the Appendix.

Because of the patchy habitat distribution, even the unfished system has a nonuniform distribution of settlers that depends on the dispersal distance (Fig. 4a, b). The distribution of habitat causes FLEP to vary between 1.0 (hard-bottom habitat) and 0.0 (not-hard-bottom habitat). This distribution of habitat determines the distribution of recruitment of species with different dispersal distances. Short-distance dispersers settle and persist at high levels in good habitat, whereas longer distance dispersers settle at slightly lower levels, but settle between the areas of good habitat. (Note, however, that settlement in non-habitat areas does not contribute to population dynamics as $FLEP = 0$.) Longer distance dispersers tend to have higher settlement where there is a higher local fraction of the coastline with good habitat, as expected from previous results on MPA network effects (Botsford et al. 2001). A plot of successful recruitment into the adult population would be constant at the saturation level in all habitat areas where settlement is greater than the 0.35 level, indicated by the dashed line in Fig. 4. Note that while settlement declines near the northern edge (left-hand side of panels), the added buffer of 200 km is more than adequate to

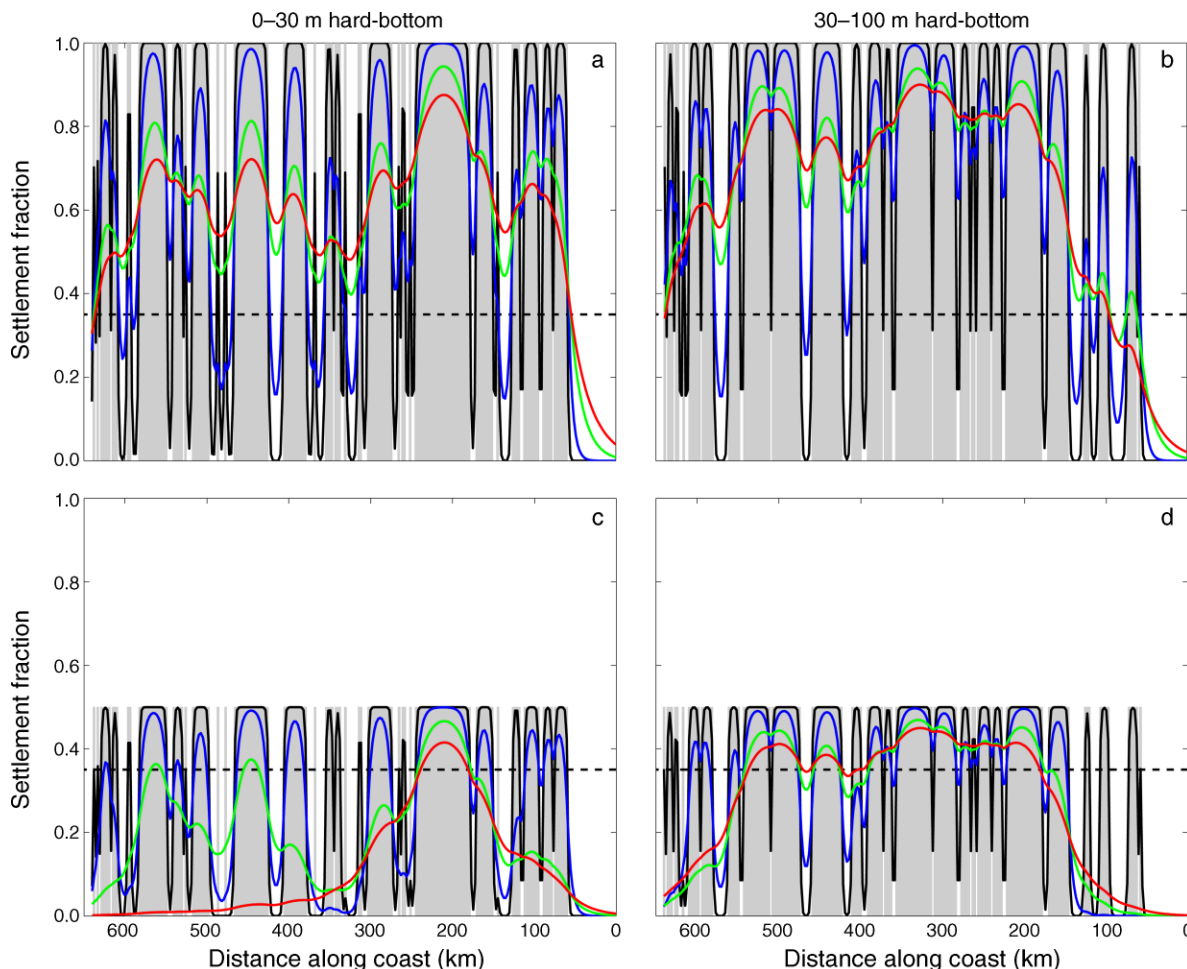


FIG. 4. Equilibrium settlement patterns for the central California coast in the absence of reserves for several different dispersal distances for (a, c) 0–30 m depth hard-bottom habitat and (b, d) 30–100 m depth hard-bottom habitat. The fraction of lifetime egg production (FLEP) in habitat areas (gray areas) is 1.0 for panels (a) and (b) and 0.5 for panels (c) and (d). Dispersal distances (km) are 1 (black), 5 (blue), 15 (green), and 25 (red). The dashed line indicates the threshold FLEP level. Note that this figure, unlike most of the figures in the paper, includes the buffer area to the north of the central California coast study region.

avoid any artificial behavior (i.e., decrease in population level due to loss of individuals at the domain boundary) in the central coast study region (50–450 km).

The effects of fishing on spatial distributions of species dispersing different distances can be calculated by adjusting the level of FLEP in habitat areas (Fig. 4c, d; Appendix: Fig. A1). As the FLEP in habitat areas is decreased (i.e., the fishing rate is increased), the spatial distribution of settlers does not decrease uniformly, but rather some areas collapse at a higher FLEP than others. This is due to spatial variations in the level of habitat fragmentation (e.g., Fahrig 2003) and the progressive collapse of populations as the exploitation rate is increased when habitat quality varies (e.g., Hutchings 1996). As a result of this spatial variability, the FLEP at which the population completely collapses in all areas depends on the habitat type and the dispersal distance (Fig. 5). In general, the value of FLEP at collapse increases with dispersal distance due to increased export

of larvae from habitat to non-habitat areas and increased loss of larvae along the system boundaries. Note that the buffer area to the north (450–650 km) minimizes the latter effect on the area of interest here (0–450 km) for the range of dispersal distances considered in *Application of the model to proposed MPA designs* (1–25 km). The value of FLEP at collapse is generally higher (i.e., occurs at a lower fishing rate) for 0–30 m hard-bottom habitat than that for 30–100 m hard-bottom habitat due to the lower overall fraction of the total area in the prior than in the latter (Table 1). Note that these results depend on the parsimonious, but difficult to validate, assumption that the threshold value of FLEP does not vary with dispersal distance or habitat type of the species.

Application of the model to proposed MPA designs

The DPR model was applied to spatial patterns of FLEP resulting from the proposed MPA configurations

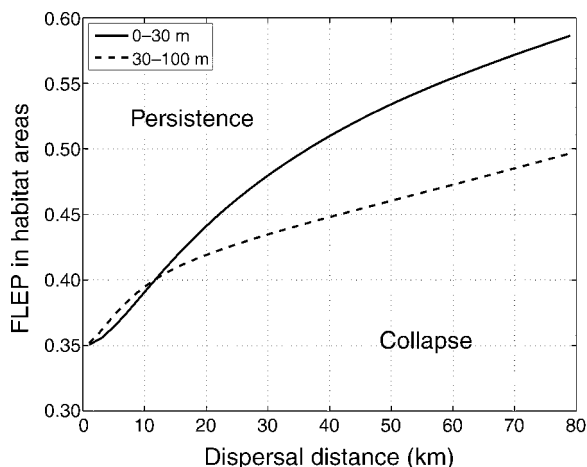


FIG. 5. The fraction of lifetime egg production (FLEP) in habitat areas below which the entire system collapses in the absence of reserves as a function of the larval dispersal distance. The solid curve is for 0–30 m depth hard-bottom habitat, and the dashed curve is for 30–100 m depth hard-bottom habitat.

to calculate spatial patterns of equilibrium settlement for four different dispersal distances. Different spatial patterns of FLEP resulted from the two different pre-reserve FLEP levels in fished areas, two assumptions about effort redistribution after MPA implementation, two habitat types, and five MPA proposals. The MPA proposals were analyzed in two ways: (1) considering only MPAs with a high level of protection (the dark gray areas in Fig. 3) and (2) considering all reserve areas (both the dark gray and light gray areas in Fig. 3). The resulting spatial patterns of equilibrium settlement were summarized in terms of the total area with settlement

greater than the threshold fraction (0.35) of natural, unfished settlement for a single isolated population.

Spatial patterns of equilibrium settlement.—Spatial patterns of equilibrium settlement were in general highly nonuniform and depended strongly on habitat type, reserve configuration, and dispersal distance. We present an example of these settlement patterns here (Fig. 6) and other cases can be found in the Appendix (Figs. A2, A3). Results varied substantially over the range of dispersal distances considered (1–25 km). Short-distance dispersers had high settlement levels in reserves of any size, but levels were much lower in the areas outside (black and blue curves of Fig. 6). For long-distance dispersers, however, there had to be a “cluster” of reserves (i.e., several reserves that occur along a length of coastline of approximately the dispersal distance) along a stretch of coastline in order for such populations to have high levels of settlement (green and red curves of Fig. 6). However, where this clustering occurred, settlement levels between the reserves in addition to within reserves were high. Another general characteristic of these results is that subtle differences in the spatial configuration of reserves and habitat can lead to large differences in the total length of coastal habitat over which long-distance dispersers will persist. For example, note that longer distance dispersers persist over a larger amount of the coastline in Fig. 6b (30–100 m depth habitat) than in Fig. 6a (0–30 m).

Summaries of persistence levels in the five MPA network proposals.—While the results shown in Fig. 6 and in the Appendix, Figs. A2 and A3, should be of interest to decision makers, they ultimately need a means of summarizing and comparing the effects of different MPA designs on the overall sustainability of the

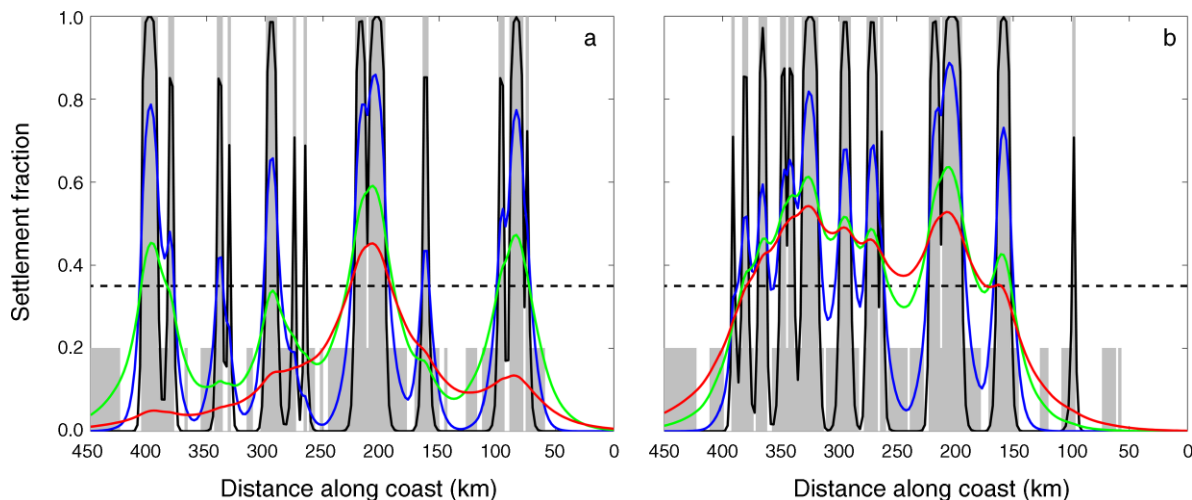


FIG. 6. Spatial patterns of equilibrium settlement levels for several dispersal distances considering all reserves areas (regardless of presumed level of protection) for two habitat types: (a) 0–30 m depth hard-bottom habitat and (b) 30–100 m depth hard-bottom habitat. Results are for the marine protected area (MPA) network proposed by the California Fish and Game Commission. Post-reserve-implementation fraction of lifetime egg production (FLEP) in non-reserve habitat areas is 0.2 in both panels. Dispersal distances (km) are 1 (black), 5 (blue), 15 (green), and 25 (red). Gray areas indicate FLEP levels, and the dashed line indicates the threshold FLEP level.

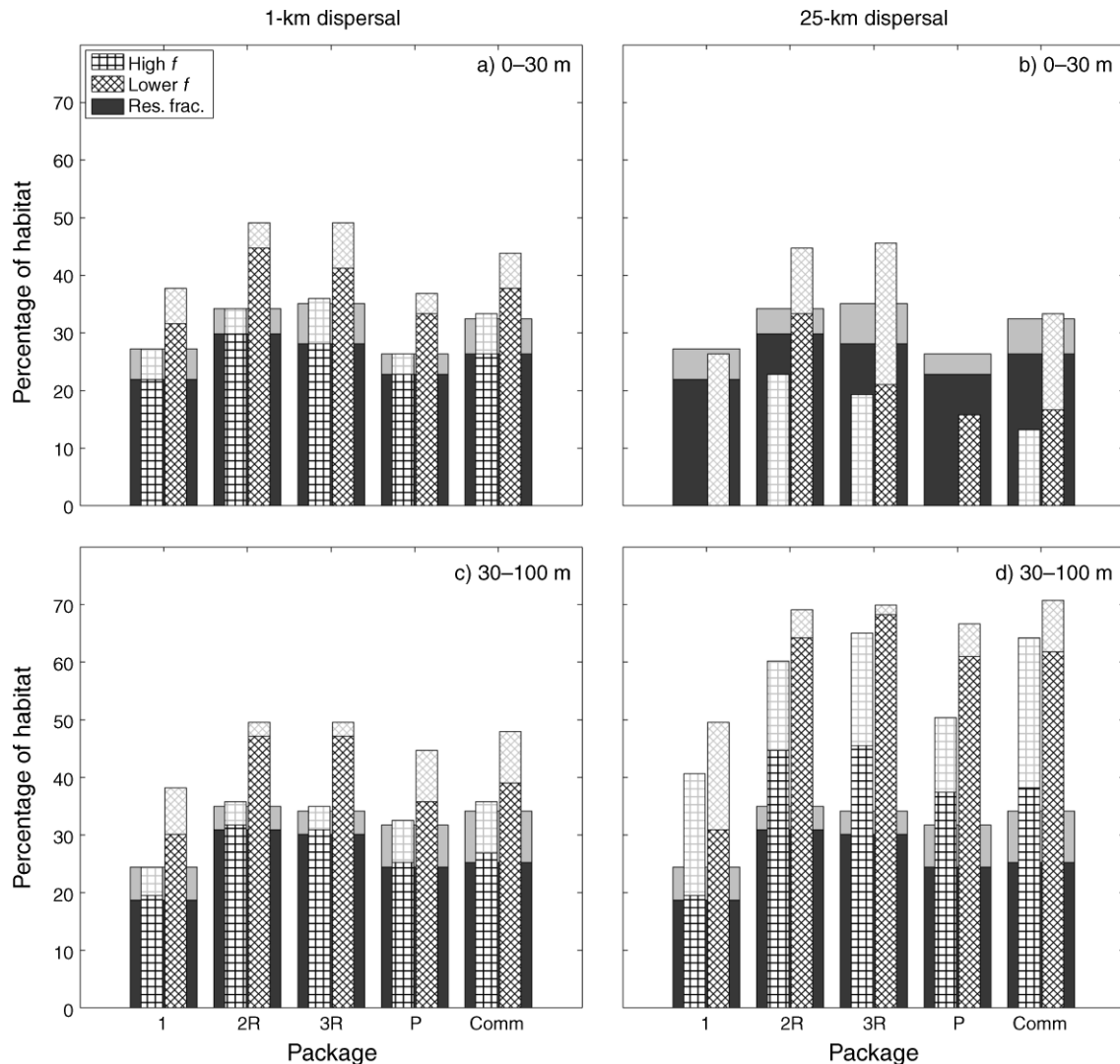


FIG. 7. Summary of persistence results for all proposed marine protected area (MPA) networks. Dispersal distances are (a, c) 1 km and (b, d) 25 km. Habitat types are (a, b) 0–30 m depth hard-bottom habitat and (c, d) 30–100 m depth hard-bottom habitat. Dark-gray bars behind hatched areas indicate percentage of habitat along central California coast in reserves classified as having a high level of protection (Res. frac.), while light-gray bars on top of dark-gray bars indicate additional areas in reserves classified as having a lower level of protection. Square-hatched bars (on the left-hand side) indicate percentage of habitat areas with settlement above the threshold fraction considering only reserves with a high level of protection for a post-reserve implementation fraction of lifetime egg production (FLEP) of 0.2 (high fishing rate, f), while diamond-hatched bars (on the right) indicate results for a FLEP of 0.3 (lower fishing rate, f). Gray-hatched bars on top of these are additional areas with settlement levels above the threshold fraction if all reserves areas, regardless of protection level, are considered.

population. Results of analyses of the five proposed MPA networks were summarized by calculating the fraction of the central California coast habitat area that had settlement above the threshold fraction (i.e., 35% of natural settlement for a single isolated population; hatched bars in Fig. 7). This represents the fraction of total habitat area for that reserve configuration that had settlement levels high enough to reach the recruitment carrying capacity. This metric provides a suitable measure of the total area for which a given network of MPAs will likely support persistent populations. This fraction can be compared to the area set aside in reserves

(broad solid gray bars in Fig. 7) as a measure of the effectiveness of this MPA network for a given dispersal distance and fishing level.

Two general patterns are clearly evident in all of the summary figures: (1) For short-distance dispersers (e.g., 1 km as in Fig. 7a, c) and a high fishing rate (FLEP of 0.2), the fraction of habitat with high levels of settlers is equal to or slightly greater than the fraction of the habitat in reserves. For a lower fishing rate (FLEP of 0.3), the fraction of habitat over which the population is persistent is somewhat higher than the fraction in reserves, but closely mirrors the fraction in reserves.

(2) For long-distance dispersers (25 km) the effectiveness of the reserve configuration does not match the amount of area set aside in MPAs, rather it is much more sensitive to the spatial configuration of reserves and habitat. For the 0–30 m hard-bottom habitat (Fig. 7b), the fraction of habitat over which species persist is generally less than the fraction of habitat in reserves, and it is zero (i.e., populations collapse) under heavy fishing pressure when one considers only reserve areas classified as highly protected. For 30–100 m hard-bottom habitat (Fig. 7d), the opposite is true, with all MPA proposals protecting more area than is in reserves.

That the fraction of habitat protected is closely tied to the fraction in reserves for short-distance dispersers is due to the self-replacement effect described in *Model development*. Since few larvae leave reserves, the only areas that receive increased recruitment are the reserves themselves. The increases in fraction protected for the lower fishing level (FLEP of 0.3) are due to small amounts of larval spillover from reserves into fished areas that are sufficient to raise settlement above 0.35 in some areas surrounding reserves.

That the proposed reserve configurations performed poorly for a dispersal distance of 25 km and 0–30 m habitat but well for 30–100 m habitat is somewhat surprising. The reason for this behavior is fundamentally due to the differences in the distributions of the two habitats (i.e., the black areas in Fig. 3). The hard-bottom habitat for 0–30 m is patchier, has larger gaps, and covers a smaller fraction of the total area (Table 1) than 30–100 m hard-bottom habitat. This makes populations inhabiting 0–30 m hard-bottom habitat less persistent in the model (see, e.g., Fig. 5) and produces collapse in a number of MPA proposals for higher fishing rates.

An alternative approach to viewing the summary information presented in Fig. 7 is given in the Appendix: Fig. A4. This method provides an indication of the “efficiency” of proposed MPA configurations by plotting the area set aside in reserves against the area with persistent populations.

Sensitivity to redistribution of fishing effort.—Persistence results for model runs in which fishing effort removed by the implementation of reserves was redistributed to non-reserve habitat areas were significantly different from results without effort redistribution (compare Fig. 7 to Fig. 8). As might be expected from the low post-reserve-implementation FLEP values in this case (Table 3), the fraction of habitat areas with high settlement levels decreased for all habitat types, proposed MPA networks, and dispersal distances. For short-distance dispersers, the persistent area was equal to the habitat area in reserves for both high and low fishing rates because the limited export from reserves combined with the FLEP in non-reserve areas was no longer sufficient to raise settlement levels above 0.35 in areas immediately outside reserves. For long-distance dispersers (25 km), effort redistribution has a particularly dramatic effect for 0–30 m hard-bottom habitat.

All proposed MPA networks collapsed unless reserves classified as having a low level of protection were also considered. Even including these reserves, only proposals 2R, 3R, and Comm have persistent populations.

DISCUSSION

The MPA network assessment method presented here is a comprehensive approach to determining the persistence of populations in different proposed spatial patterns of marine reserves in that it accounts for spatial patterns of habitat and fishing effort (as reflected in reproductive output, FLEP) and the connectivity due to larval dispersal. The approach includes most, but not all, essential elements of fish population dynamics with MPAs. The results of this application of the method also extend our general understanding of spatial dynamics of populations.

The results for persistence in the model system in the absence of reserves indicate that in the un-fished state, we would see little difference between short-distance dispersers and long-distance dispersers. They would persist in all available habitat, as modeled here. Their responses to fishing, however, differ due to differences in habitat distribution and larval dispersal distance. These results highlight one interesting issue related to translating fishery models from a nonspatial to a spatial context. Though the settler–recruit relationship is nominally configured so that an isolated single population will collapse at a FLEP of 0.35, the actual model system collapses at higher FLEP values (Fig. 5) because of the existence of non-habitat areas and the finite coastline of the model system. The use of the threshold FLEP value of 0.35 is based on meta-analyses of regional fisheries (Mace and Sissenwine 1993, Myers et al. 1999) that in principle already include some of these losses. This suggests that the actual local threshold settlement rate in habitat areas may be lower than 0.35 so that the threshold of the entire system remains 0.35. However, for most fish species there is little information about local density-dependent effects that would justify the use of some other threshold value. In the absence of such information, we have made the conservative choice to keep the threshold value constant at 0.35. Nonetheless, the study of the factors that drive local density-dependent effects remains an interesting avenue for future research.

The major result notable in Figs. 6, 7, and 8 is that long-distance dispersers are more sensitive to MPA design and the spatial distribution of habitat. The mechanism underlying this conclusion follows from the network effect described in Botsford et al. (2001), whereby persistence at long dispersal distances will only occur if the total area in reserves is above some critical fraction. Kaplan et al. (2006) provided a simple expression in terms of the fishing rate in non-reserve areas and the threshold value of FLEP for the minimum fraction of the total area that needs to be placed in reserves to guarantee persistence for all dispersal

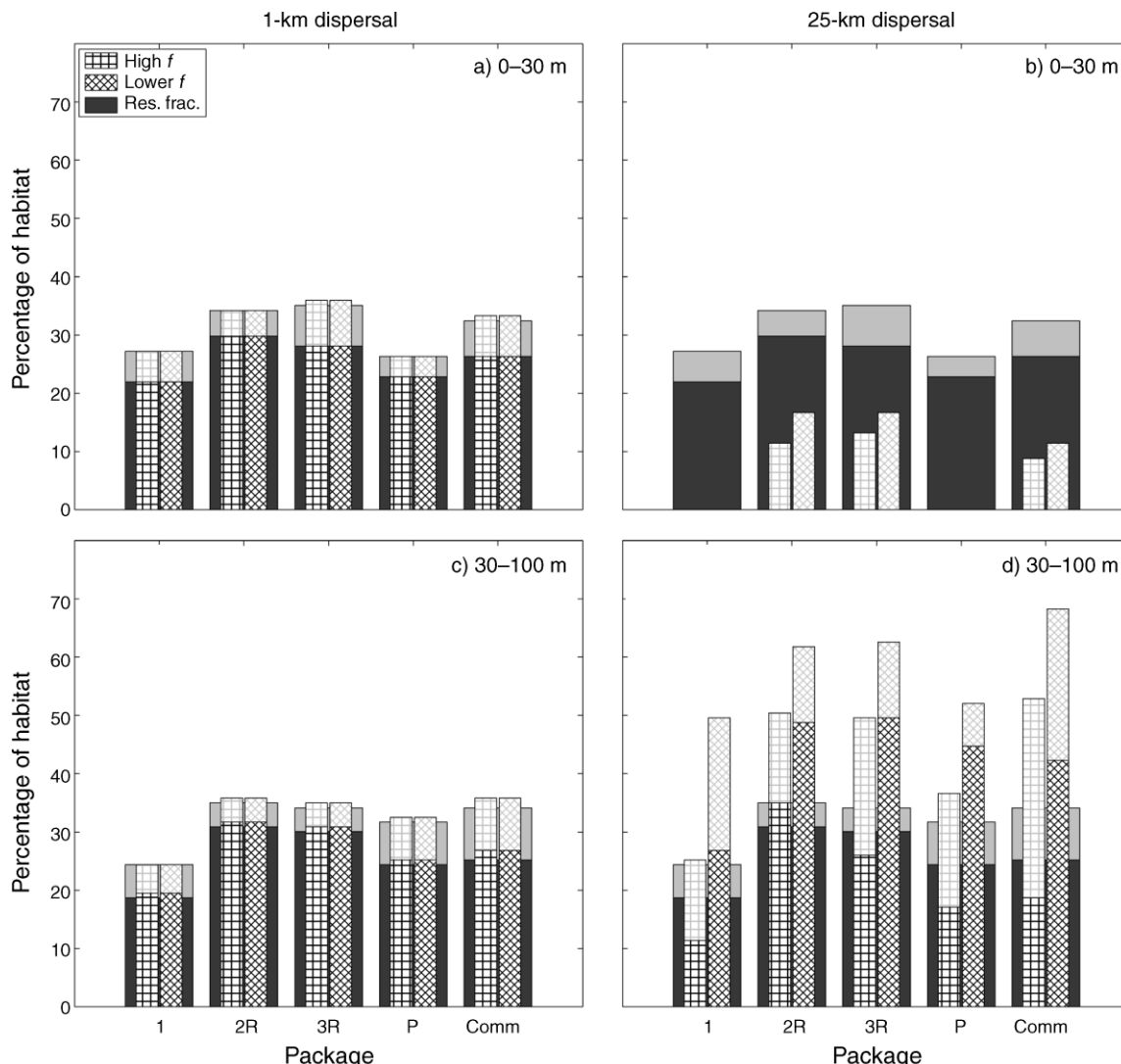


FIG. 8. Summary of persistence results for all proposed marine protected area (MPA) networks when effort is redistributed after reserve implementation. Panels are as in Fig. 7 with the exception that fraction of lifetime egg production (FLEP) levels of 0.2 and 0.3 are pre-reserve-implementation FLEP levels.

distances on an infinite coastline with uniform habitat. This result can easily be extended to coastlines with nonuniform habitat

$$P \geq \frac{f_{sat} - FLEP}{1 - FLEP} \quad (3)$$

where P is the fraction of habitat areas in reserves, C is the fraction of the coastline that is habitat, and f_{sat} is the threshold fraction of natural settlement. Though this relationship only holds exactly for an infinite coastline, it is approximately valid for any section of coastline that is considerably larger than the dispersal distance (so that edge effects are relatively minor). This explains why persistence results differ significantly for the two habitat types considered here for long-distance dispersers. The

global fraction of habitat in reserves (Table 2) is slightly less than that necessary to guarantee persistence (Fig. 9), and, therefore, one expects significant differences in persistence of long-distance dispersers due to small changes in either the fraction of coastline that is habitat or the fraction of habitat in reserves.

As some of the species of interest here, particularly many rockfish species, may have mean dispersal distances greater than 25 km, the question has been raised whether persistence would improve if longer dispersal distances (i.e., greater than 25 km) were considered. In particular, it has been suggested that longer dispersal distances would generate increased connectivity among reserves and, thereby, produce increased persistence. This is not the case, however, as has been demonstrated in a number of different ways

(Hastings and Botsford 1999, 2006, Kaplan et al. 2006). If dispersal is solely a diffusive process that is peaked around the point of larval production (e.g., does not incorporate alongshore advection), then populations will always collapse at a large dispersal distance if they collapse at an intermediate dispersal distance (Kaplan et al. 2006). One way to understand this result is that for short-distance dispersers, larvae produced in reserves have a high chance of settling in the reserve, while for long-distance dispersers the chance of settling in a reserve is roughly the percentage of total area in reserves (a smaller number). Therefore, the chance of settlement in reserves, which increases the LEP of settlers and is directly related to the overall persistence of the system, always decreases as dispersal distance is increased. In fact, the population level will always go to zero above some dispersal distance if the average reproductive output of fished areas and reserve areas is below the threshold settlement level (Kaplan et al. 2006; Eq. 3). On the other hand, if the average reproductive output is above the threshold level, persistence is guaranteed at long dispersal distances. This is the fundamental difference between 0–30 m and 30–100 m hard-bottom habitat. The increased patchiness and lower overall fraction of the total area in 0–30 m hard-bottom habitat yields a total reproductive output that is below the replacement level and, therefore, produces collapse at long dispersal distances.

The principal goal of the results obtained here is to provide scientific support for design and decision-making for the implementation of MPA networks. The summaries of persistence and the spatial maps of settlement produced by the method provide useful tools during the design phase of an MPA network. For example, the poor performance of long-distance dispersers in packages 1 and P at a high fishing rate (FLEP of 0.2) in the 0–30 m depth range can be traced to the lack of persistence between 180 and 230 km (see Appendix: Fig. A2a, d as compared to Fig. A2b, c, e). Tracing that location back to the reserve configurations in Fig. 3a reveals that there is less coastline in reserves in that area. If desired, this shortcoming could be remedied, for example, by replacing the configuration of reserves in package 1 or P between 180 and 230 km by that of package 3R. Proposed MPAs could be moved or new ones could be proposed, and their effects on populations could be seen immediately if this DPR approach were used in a workshop setting. The MPA design for multiple species and/or habitat types would be achieved by comparing the results of multiple DPR runs for the different configurations. Computer-based optimization of this process has not yet been achieved, but is a desirable goal for future work.

Summaries of results as in Figs. 7 and 8 and Appendix: Fig. A4 would be useful in the selection of the best package by decision makers and for combined management that includes effort-based controls and MPAs. For example, under intensive fishing, packages

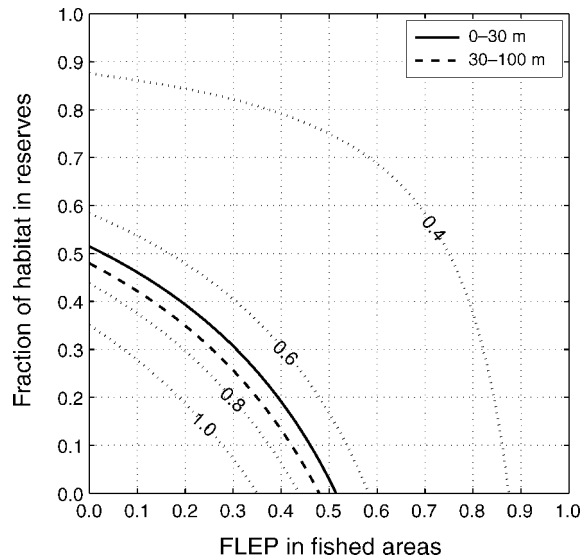


FIG. 9. Fraction of habitat in reserves above which persistence is guaranteed for larval pool dispersal on an infinite coastline as a function of fraction of lifetime egg production (FLEP) in fished habitat areas for several different fractions of the total area that is habitat. The fraction of total area in habitat is indicated on the dotted curves for several reference fractions, while the solid and dashed curves are the results for the fractions in habitat shown in Table 1 (without buffers) for 0–30 m depth and 30–100 m depth hard-bottom habitat, respectively.

2R and 3R would likely be selected because they perform best for the sensitive long-distance dispersers (Fig. 7b). Alternatively, decision-makers could choose to reduce fishing outside MPAs, in which case packages 1 and P could be considered adequate (Appendix: Fig. A4b, d).

The method described and demonstrated here also provides a starting point for expectations that could form the basis of MPA monitoring efforts. Adaptive management requires predictions against which performance can be measured. While the predicted patterns of equilibrium settlement provided here are not intended to precisely reproduce the final state of the population, they provide a sound basis for comparison with the results of monitoring efforts and for improving the design of MPAs. For example, if package Comm were implemented, one would expect to find a gradient in abundance of long-distance dispersers that inhabit depths between 0 m and 30 m, peaking near 200 km and declining in either alongshore direction.

Comparison of the assessment method presented here with other rule- or habitat-based assessment methods shows that there are many aspects of the dynamics of the system that cannot be ascertained without using a model-based approach. For example, the rule-based method used in the central California MPA process specified that MPAs should be a minimum of 5–10 km in alongshore width (with 10–20 km preferred) and be no more than 50–100 km apart (California Department

of Fish and Game, Marine Life Protection Act Initiative, *available online*).⁹ These guidelines were chosen on the basis of quantitative estimates of the distribution of ranges of larval and juvenile/adult movement for local species in the context of expected average responses to MPA size (Kellner et al. 2007) and spacing (derived from Botsford et al. 2001). This rule-based method does not account for the spatial distribution of habitat, which also affects sustainability of populations, as demonstrated in Fig. 5. For example, it did not reflect the fact that persistence of all packages was low in the 0–30 m hard-bottom habitat for long-distance dispersers. The rule-based method also does not lend itself to mixed fisheries management that explicitly includes both reserves and controls on fishing effort. In these cases, Eq. 3 may provide a more useful rule of thumb for the initial design of MPA proposals than specifying universal MPA size and spacing guidelines as it combines the fraction in reserves with the fishing rate and the distribution of habitat.

Similar limitations apply to habitat-based MPA assessment systems, such as MARXAN (Ball and Possingham 2000, Possingham et al. 2000), that include the distribution of habitats but do not address the connectivity between habitat patches or the consequences of anthropogenic activities. However, the results obtained here also have implications for how connectivity might be included as a criterion in habitat-based evaluations. Including iterative solutions to obtain population equilibria for species dispersing a variety of distances would most likely be prohibitively time-consuming in the search routines used to dynamically design a MPA network. However, the result obtained here, that persistence is most sensitive to long-distance dispersers, suggests that a single indicator reflecting their connectivity could be a useful addition to such habitat-based approaches.

Walters et al. (2007) formulated a model of this same implementation process in California and concluded that MPAs would be substantially less effective when adult movement was accounted for in the model. They represented adult movement as a diffusive process occurring throughout the lifetime of adult individuals, rather than as movement within a home range, which is the case for many of the species of interest here (e.g., see Starr et al. 2005, Jorgensen et al. 2006). Moreover, they also chose rates of adult movement that are greater than those observed, which caused excessive spillover of adults from reserve areas into fished areas and led to little benefit for most species as a result of MPA implementation. Their conclusion that the size and configuration of MPAs has little impact on achieving the goals of these MPAs also stems from their assumption of an inordinately high level of adult movement. They further concluded that achieving the goals of the

California MPA implementation process depends on fisheries management outside reserves, which agrees with our results and is consistent with earlier results regarding the corresponding effects of conventional and spatial management (e.g., Holland and Brazeel 1996, Mangel 1998, Hastings and Botsford 1999).

Caveats regarding the fidelity of our model outcomes fall into two categories: those that can be remedied soon in future models and those that depend on a fundamental lack of a scientific understanding of basic processes. Assumptions regarding dispersal and early life history are perhaps the most critical assumptions in the latter category. Dispersal patterns are generally not known except for species with larval durations on the order of days. Yet persistence is sensitive to several aspects of larval dispersal, such as the existence and strength of an advective component in the larval distribution (Gaylord and Gaines 2000, Botsford et al. 2001, Kaplan 2006). While we have not explicitly included larval advection in this model, the effects of alongshore transport of larvae are not entirely unpredictable. In Kaplan (2006), it was shown that alongshore advection, or any other process that reduces retention of larvae in reserves and increases transport of larvae from reserves to fished areas, will reduce the overall persistence of the system. Reductions can be significant if few larvae produced in reserves are unable to recruit back to reserve areas. In this context, the results for persistence presented here that do not include alongshore advection are likely to be optimistic compared to those that would be observed if there is a significant net alongshore transport of larvae. Kaplan (2006) also explored in a theoretical context the issue of temporal variability by adding Gaussian noise to dispersal and found that a long-term equilibrium was approached that is approximately the same as that of the system with a constant dispersal pattern whose width is somewhat larger than the long-term mean dispersal pattern. Therefore, we view our representation of dispersal and our predictions of persistence as reasonable averages over the effects of temporal variability.

The type of density dependence in early life has a substantial effect on persistence. We assumed an intra-cohort, post-dispersal relationship between recruits and settling larvae, but persistence could have been greater with post-dispersal adult dependence (Gaylord et al. 2005, Ralston and O'Farrell 2008) or less with pre-dispersal density dependence (Parrish 1999, Gardmark et al. 2006). These factors determine the value of the threshold necessary for persistence and how it should be employed. Furthermore, the precise value of the recruitment threshold to use, particularly in a spatial context, is highly debatable. The actual threshold value for a specific species may be lower or higher than the value used here (0.35), but the salient feature of our results, namely that persistence of overfished species with long dispersal distances is more sensitive to habitat distribution and area in reserves, is robust to changes in the threshold value.

⁹ (<http://www.dfg.ca.gov/MRD/mlpa/>)

Movement of juvenile and adult fish and more complicated movement by fishers in response to implementation of MPAs are factors for which substantial information exists, but further analysis and modeling is required. By omitting movement of juvenile and adult fish we have essentially assumed that the spatial scales of that movement are small compared to the size of reserves over the lifetime of an average fish. As discussed here, adult movement will tend to increase spillover of fish inside reserves to fished areas, thereby potentially benefiting fisheries yield at the expense of reducing the protection level of reserves and, consequently, the persistence of the MPA system. Furthermore, ontogenic movements of some fish species from shallower to deeper habitats with age may take older individuals outside of narrow, coastal reserve areas and, therefore, reduce MPA protection levels for those species.

With regard to the behavior of fishers, the case we have considered, a uniform redistribution of fishing effort after reserve implementation, is likely extreme as some fishers may drop out and optimal distributions will concentrate fishers along the edge of the reserve if adults move (Kellner et al. 2007). Generally, the response of fishers is likely to be more complex given the nonuniform population densities predicted by the spatial patterns of settlement (Fig. 6) and by adult spillover from reserves. The precise effects of fisher and adult fish behavior will depend on the spatial scales of adult spillover and fishers' responses to this spillover (Kellner et al. 2007).

One major improvement we are pursuing that should make our approach more useful is explicit representation in two dimensions. This will improve visual accessibility and hence usefulness in stakeholder workshops and comprehension by decision makers. However, a fully two-dimensional description of the system will require more realistic patterns of larval dispersal and will introduce new spatial aspects of population behavior, such as the question of how to assess and account for offshore transport of larvae in the model configuration. Furthermore, accounting for adult movement in such a two-dimensional model will require representing the ontogenetic movements of many rockfish species.

Though the model developed here has ample room for future development, we emphasize that it includes the most essential aspects of the system and provides a consistent, comprehensive, and efficient means of evaluating MPA designs. Further development, including the eventual 2-D MPA model, should provide a valuable tool for future scientific assessments of MPA designs.

ACKNOWLEDGMENTS

This work was supported by a grant from the Resource Legacy Fund Foundation. The authors thank the science advisory team to the California MLPA process, Steve Ralston,

and two anonymous reviewers for all of their many helpful comments and suggestions.

LITERATURE CITED

- Airame, S., J. E. Dugan, K. D. Lafferty, H. Leslie, D. A. McArdle, and R. R. Warner. 2003. Applying ecological criteria to marine reserve design: a case study from the California Channel Islands. *Ecological Applications* 13: S170–S184.
- Allison, G. W., S. D. Gaines, J. Lubchenco, and H. P. Possingham. 2003. Ensuring persistence of marine reserves: catastrophes require adopting an insurance factor. *Ecological Applications* 13:S8–S24.
- Ball, I. R., and H. P. Possingham. 2000. MARXAN (v1.8.2): marine reserve design using spatially explicit annealing. (http://www.uq.edu.au/marxan/docs/marxan_manual_1_8_2.pdf)
- Barrowman, N. J., and R. A. Myers. 2000. Still more spawner–recruitment curves: the hockey stick and its generalizations. *Canadian Journal of Fisheries and Aquatic Sciences* 57:665–676.
- Bell, J. J., and B. Okamura. 2005. Low genetic diversity in a marine nature reserve: re-evaluating diversity criteria in reserve design. *Proceedings of the Royal Society B* 272: 1067–1074.
- Botsford, L. W. 1997. Dynamics of populations with density-dependent recruitment and age structure. Pages 371–408 *in* S. Tuljapurkar and H. Caswell, editors. *Structured population models in marine, terrestrial, and freshwater systems*. Chapman and Hall, New York, New York, USA.
- Botsford, L. W., A. Hastings, and S. D. Gaines. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters* 4:144–150.
- Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*. Sinauer, Sunderland, Massachusetts, USA.
- Clark, W. G. 2002. F-35% revisited ten years later. *North American Journal of Fisheries Management* 22:251–257.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics* 34:487–515.
- Gaines, S. D., S. Lester, G. Eckert, B. Kinlan, R. Sagarin, and B. Gaylord. 2008. Dispersal and geographic ranges in the sea. *In* J. Witman and K. Roy, editors. *Marine macroecology*. University of Chicago Press, Chicago, Illinois, USA, *in press*.
- Gardmark, A., N. Jonzen, and M. Mangel. 2006. Density-dependent body growth reduces the potential of marine reserves to enhance yields. *Journal of Applied Ecology* 43:61–69.
- Gaylord, B., and S. D. Gaines. 2000. Temperature or transport? Range limits in marine species mediated solely by flow. *American Naturalist* 155:769–789.
- Gaylord, B., S. D. Gaines, D. A. Siegel, and M. H. Carr. 2005. Marine reserves exploit population structure and life history in potentially improving fisheries yields. *Ecological Applications* 15:2180–2191.
- Gladstone, W. 2007. Requirements for marine protected areas to conserve the biodiversity of rocky reef fishes. *Aquatic Conservation—Marine and Freshwater Ecosystems* 17:71–87.
- Goodyear, C. P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *Canadian Special Publications in Fisheries and Aquatic Science* 120:67–81.
- Hastings, A., and L. W. Botsford. 1999. Equivalence in yield from marine reserves and traditional fisheries management. *Science* 284:1537–1538.
- Hastings, A., and L. W. Botsford. 2006. Persistence of spatial populations depends on returning home. *Proceedings of the National Academy of Sciences (USA)* 103:6067–6072.

- Holland, D., and R. Braze. 1996. Marine reserves for fisheries management. *Marine Resource Economics* 11:157–171.
- Hutchings, J. A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. *Canadian Journal of Fisheries and Aquatic Sciences* 53:943–962.
- Jorgensen, S. J., D. M. Kaplan, A. P. Klimley, S. G. Morgan, M. R. O'Farrell, and L. W. Botsford. 2006. Limited movement in blue rockfish (*Sebastes mystinus*): internal structure of the home range. *Marine Ecology Progress Series* 327:157–170.
- Kaplan, D. M. 2006. Alongshore advection and marine reserves: consequences for modeling and management. *Marine Ecology Progress Series* 309:11–24.
- Kaplan, D. M., L. W. Botsford, and S. Jorgensen. 2006. Dispersal per recruit: an efficient method for assessing sustainability in marine reserve networks. *Ecological Applications* 16:2248–2263.
- Kellner, J., I. Tetreault, S. D. Gaines, and R. M. Nisbet. 2007. Fishing the line near marine reserves in single and multispecies fisheries. *Ecological Applications* 17:1039–1054.
- Kinlan, B., and S. D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84:2007–2020.
- Kinlan, B. P., S. D. Gaines, and S. E. Lester. 2005. Propagule dispersal and the scales of marine community process. *Diversity and Distributions* 11:139–148.
- Lockwood, D. R., A. Hastings, and L. W. Botsford. 2002. The effects of dispersal patterns on marine reserves: Does the tail wag the dog? *Theoretical Population Biology* 61:297–309.
- Lombard, A. T., et al. 2007. Conserving pattern and process in the Southern Ocean: designing a marine protected area for the Prince Edward Islands. *Antarctic Science* 19:39–54.
- Love, M. S., M. Yoklavich, and L. Thorsteinson. 2002. *The rockfishes of the northeast Pacific*. University of California Press, Berkeley, California, USA.
- Mace, P. M., and M. P. Sissenwine. 1993. How much spawning per recruit is enough? *Canadian Special Publication of Fisheries and Aquatic Sciences* 120:101–118.
- Mahevas, S., and D. Pelletier. 2003. ISIS-Fish, a generic and spatially explicit simulation tool for evaluating the impact of management measures on fisheries dynamics. *Ecological Modelling* 171:65–84.
- Mangel, M. 1998. No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. *Ecology Letters* 1:87–90.
- Meester, G. A., A. Mehrotra, J. S. Ault, and E. K. Baker. 2004. Designing marine reserves for fishery management. *Management Science* 50:1031–1043.
- Miller, J. A., and A. L. Shanks. 2006. Evidence for limited larval dispersal in black rockfish (*Sebastes melanops*): implications for population structure and marine reserve design. *Canadian Journal of Fisheries and Aquatic Sciences* 61:1723–1735.
- Myers, R. A., K. G. Bowen, and N. J. Barrowman. 1999. Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences* 56:2404–2419.
- O'Farrell, M. R., and L. W. Botsford. 2005. Estimation of change in lifetime egg production from length frequency data. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1626–1639.
- O'Farrell, M. R., and L. W. Botsford. 2006. The fisheries management implications of maternal-age-dependent larval survival. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2249–2258.
- Parrish, R. 1999. Marine reserves for fisheries management: Why not? *California Cooperative Oceanic Fisheries Investigations* 40:77–86.
- Possingham, H. P., I. R. Ball, and S. Andelman. 2000. Mathematical methods for identifying representative reserve networks. Pages 291–305 in S. Ferson and M. Burgman, editors. *Quantitative methods for conservation biology*. Springer-Verlag, New York, New York, USA.
- Ralston, S., and M. R. O'Farrell. 2008. Spatial variation in fishing intensity and its effect on yield. *Canadian Journal of Fisheries and Aquatic Sciences* 65:588–599.
- Sala, E., O. Aburto, G. Paredes, I. Parra, J. C. Barrera, and P. K. Dayton. 2002. A general model for designing networks of marine reserves. *Science* 298:1991–1993.
- Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* 13:S159–S169.
- Shepherd, J. G. 1982. A versatile new stock–recruitment relationship for fisheries, and the construction of sustainable yield curves. *ICES Journal of Marine Science* 40:67–75.
- Sissenwine, M. P., and J. G. Shepherd. 1987. An alternative perspective on recruitment overfishing and biological reference points. *Canadian Journal of Fisheries and Aquatic Sciences* 44:913–918.
- Smith, M. D., and J. E. Wilen. 2003. Economic impacts of marine reserves: the importance of spatial behavior. *Journal of Environmental Economics and Management* 46:183–206.
- Starr, R. M., V. O'Connell, S. Ralston, and L. Breaker. 2005. Use of acoustic tags to estimate natural mortality, spillover, and movements of lingcod (*Ophiodon elongatus*) in a marine reserve. *Marine Technology Society Journal* 39:19–30.
- Walters, C. J., R. Hilborn, and R. Parrish. 2007. An equilibrium model for predicting the efficacy of marine protected areas in coastal environments. *Canadian Journal of Fisheries and Aquatic Sciences* 64:1009–1018.
- Wares, J., S. D. Gaines, and C. Cunningham. 2000. A comparative study of asymmetric migration events across a marine biogeographic boundary. *Evolution* 55:295–306.

APPENDIX

Additional figures, including spatial patterns of equilibrium settlement for each proposed marine protected area (MPA) network, habitat type, and fraction of lifetime egg production (FLEP) level (*Ecological Archives* A019-018-A1).