

# Decision analysis for designing marine protected areas for multiple species with uncertain fishery status

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**Abstract.** Marine protected areas (MPAs) are growing in popularity as a conservation tool, and there are increasing calls for additional MPAs. Meta-analyses indicate that most MPAs successfully meet the minimal goal of increasing biomass inside the MPA, while some do not, leaving open the important question of what makes MPAs successful. An often-overlooked aspect of this problem is that the success of fishery management outside MPA boundaries (i.e., whether a population is overfished) affects how well MPAs meet both conservation goals (e.g., increased biomass) and economic goals (e.g., minimal negative effects on fishery yield). Using a simple example of a system with homogeneous habitat and periodically spaced MPAs, we show that, as area in MPAs increases, (1) conservation value (biomass) may initially be zero, implying no benefit, then at some point increases monotonically; and (2) fishery yield may be zero, then increases monotonically to a maximum beyond which further increase in MPA area causes yield to decline. Importantly, the points at which these changes in slope occur vary among species and depend on management outside MPAs. Decision makers considering the effects of a potential system of MPAs on multiple species are confronted by a number of such cost–benefit curves, and it is usually impossible to maximize benefits and minimize costs for all species. Moreover, the precise shape of each curve is unknown due to uncertainty regarding the fishery status of each species. Here we describe a decision-analytic approach that incorporates existing information on fishery stock status to present decision makers with the range of likely outcomes of MPA implementation. To summarize results from many species whose overfishing status is uncertain, our decision-analysis approach involves weighted averages over both overfishing uncertainty and species. In an example from an MPA decision process in California, USA, an optimistic projection of future fishery management success led to recommendation of fewer and smaller MPAs than that derived from a more pessimistic projection of future management success. This example illustrates how information on fishery status can be used to project potential outcomes of MPA implementation within a decision analysis framework and highlights the need for better population information.

**Key words:** California, USA; decision analysis; decision support; fishery stock status; fishery yield; marine protected area (MPA); metapopulation persistence; overfishing; spatially explicit population model.

## INTRODUCTION

Marine protected areas (MPAs) are an increasingly popular tool for marine conservation and management. While several recent studies have touted the benefits of MPA implementation for population sustainability, biodiversity, and ecosystem services (Mumby et al. 2006, Worm et al. 2006), not all MPAs realize their intended goals. In fact, meta-analyses reveal that some MPAs have had neutral or negative effects on local populations and ecosystems (Halpern 2003, Guidetti and Sala 2007, Lester et al. 2009). For example, Halpern (2003) found that in only 63% of cases were population densities higher inside than outside MPA boundaries.

Given this uncertainty about the potential benefits of MPAs and the parallel concerns of fishers about lost fishing grounds and revenues, MPA design is a politically contentious process (Airamé et al. 2003, Hilborn et al. 2004). Policy makers often seek advice from scientists on the potential biological benefits (e.g., improved sustainability) and economic costs (e.g., reduced fishery yield) of proposed MPAs, relative to existing management, and scientists providing “decision support” must grapple with the difficulty of making predictions in the face of uncertainty (Halpern et al. 2006, Hill et al. 2007).

The wide range of anticipated consequences of MPAs reflects a fundamental uncertainty associated with MPAs, and such a range suggests a need to understand those consequences better (Sale et al. 2005). Most advocates of MPAs believe that they will improve sustainability and catch, while many fishers anticipate an obvious decline in catch, at least in the short term.

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The major factors leading to this uncertainty have been identified (Botsford et al. 2003) as (1) limited knowledge of connectivity within marine metapopulations (Botsford et al. 2008, 2009) and (2) lack of information regarding the conditions under which marine populations will become unsustainable (i.e., species resilience; Botsford et al. 2001, Hastings and Botsford 2006). The latter is especially important because it is the same source of uncertainty that hinders conventional fisheries management (Botsford et al. 2001), i.e., the relationship between annual recruitment and reproduction at low density (also known as “steepness” or the compensation ratio; Hilborn and Walters 1992). Here we focus primarily on this second type of uncertainty in MPA design, which is essentially uncertainty regarding how much fishing a population can support before collapsing. However, we also explore how different larval dispersal distances and home range sizes (the first type of uncertainty) affect MPA outcomes.

Existing strategic, theoretical studies indicate that the impact of MPAs on fisheries depends on conventional fishery management outside MPA boundaries, and available empirical evidence supports this finding (Micheli et al. 2004). Because the primary effect of most MPAs is to eliminate fishing pressure on organisms inside the MPA, MPAs can have an effect on fishery yield that is approximately equivalent to reducing harvest rates using conventional, nonspatial management (Mangel 1998, 2000, Hastings and Botsford 1999; but see White and Kendall 2007, Ralston and O’Farrell 2008 for exceptions). Therefore, placing a certain fraction of the coastline in MPAs may ensure persistence and improve fishery yields for a population that is severely overfished outside of the MPAs and would otherwise collapse (Hastings and Botsford 1999, Botsford et al. 2001, Gaylord et al. 2005, White and Kendall 2007), but MPAs may simply reduce fishing opportunities and yield if the stock is already managed sustainably (Holland and Brazeel 1996, Mangel 1998, 2000, Hastings and Botsford 1999, Sladek-Nowlis and Roberts 1999, Ralston and O’Farrell 2008). Consequently, the predicted benefits (or costs) of a proposed MPA for a fishery should depend on knowledge about both the current status of the stock and how it will be managed in the future.

Unfortunately, estimates of a fishery’s overfishing status are notoriously uncertain. Stock status is generally quantified in terms of population abundance and lifetime egg production (LEP) of recruits (Sissenwine and Shepherd 1987, Goodyear 1993; see Table 1 for a summary of abbreviations used in this paper). The latter metric is a common currency that affects the performance of both MPAs and conventional fisheries (where it is known more commonly as egg-per-recruit, EPR). Fishing truncates the size structure of a population by removing older, larger individuals, and the effects of fishing on persistence can be described by the fraction of natural, unfished lifetime egg production (FLEP) that will be realized by new recruits (Sissenwine

and Shepherd 1987, O’Farrell and Botsford 2005). Determining the threshold fishing rate that will ensure a sustainable stock requires estimation of how the current fishing rate affects population replacement, in terms of FLEP, and estimation of the critical replacement threshold (CRT) below which FLEP is too low to ensure replacement. At equilibrium, the number of recruits is given by the point at which the egg–recruit curve intersects with a line that begins at the origin and has slope  $1/\text{FLEP}$ . The slope of the egg–recruit curve at the origin is  $1/\text{CRT}$ , so if  $\text{FLEP} < \text{CRT}$ , the equilibrium is zero recruits and the population collapses (Sissenwine and Shepherd 1987). This is similar to estimation of  $R_0$  in linear (non-density-dependent) populations (Caswell 2001). Just as  $R_0$  must exceed 1.0 for population persistence (at this threshold, each adult replaces itself with exactly one offspring within its lifetime), FLEP must exceed the CRT for the population to replace itself. The concept of maintaining FLEP greater than CRT is essentially the same as the goal in conventional fisheries management of maintaining spawning potential ratio (SPR) greater than a specified threshold percentage, though the rationale is slightly different (at least on the west coast of the United States), in that the targeted SPR threshold is intended to be a proxy for maximum sustained yield (MSY), not a persistence threshold (Clark 1991, 2002, Ralston 2002). Note that several other quantities have been defined to describe the slope of the egg–recruit curve at low abundance, such as the compensation ratio and steepness (Hilborn and Walters 1992, Martell et al. 2008; Table 1). This slope can only be estimated accurately after a population has been reduced to very low abundance. This difficulty leads to uncertainty regarding the actual status of a fishery.

An example of the uncertainty associated with overfishing status and MPA design arises on the Pacific coast of the United States, where rockfish (*Sebastes* spp., Scorpaenidae) are a taxon of great interest for protection in MPAs. At present, rockfish stock assessments are based in part on a hierarchical Bayesian estimation of the egg–recruitment slope parameter for each species (e.g., Dorn 2002). The original management goal for rockfish was a value of FLEP that was 35% of the natural, unfished LEP (Ralston 2002; note that Ralston and other fisheries biologists typically refer to EPR rather than LEP; the two quantities are equivalent but estimated differently; Table 1; Goodyear 1993, O’Farrell and Botsford 2005). After a number of the stocks collapsed to undesirably low levels (Ralston 1998), the recommended level of FLEP was increased to 50% or more (Clark 2002, Dorn 2002, Ralston 2002). However, stock assessments continue to estimate the CRT for these stocks as a much lower value and use that value to calculate harvest limits. This situation leads to a range of viewpoints regarding the status of these stocks. For example, O’Farrell and Botsford (2006) analyzed the size struc-

TABLE 1. Terms and abbreviations used in the paper.

Abbreviation	Name	Definition
CRT†	critical replacement threshold	Minimum value of FLEP required for population persistence without MPAs. Inverse of the slope at the origin of the egg–recruit relationship.
DPR	dispersal per recruit	Method for simulating population dynamics using the spatial distribution of larval settlers expected to be produced by each successful recruit (Kaplan et al. 2006).
EPR‡	eggs per recruit	Average lifetime reproductive effort of a new recruit. Equivalent to LEP, but usually calculated in a different way (Hilborn and Walters 1992).
FLEP§	fraction of lifetime egg production	Fraction of unfished LEP realized by a fished population. Conceptually identical to SPR, but calculated in a manner that is less sensitive to estimates of the natural mortality rate (O’Farrell and Botsford 2005).
LEP‡	lifetime egg production	Average lifetime reproductive effort of a new recruit. Equivalent to EPR, but usually calculated in a different way (O’Farrell and Botsford 2005).
MPA	marine protected area	Spatial unit in which fishing is restricted or prohibited.
MSY	maximum sustainable yield	Maximum fishery yield possible at equilibrium.
SPR§	spawning potential ratio	The ratio of spawning stock biomass in a fished population to that of an unfished population (Goodyear 1993).
YPR	yield per recruit	Mean biomass yield resulting from a single new recruit (Kaplan et al. 2006).
Other definitions:		
	compensation ratio†	A measure of the slope at the origin of the egg–recruit relationship. Defined as the ratio of recruitment at FLEP = 0 divided by recruitment at FLEP = 1 (Goodyear 1980); equal to 1/CRT.
	slope at the origin†	The slope at the origin of the egg–recruit or stock–recruit relationship. In a population without MPAs, FLEP must exceed the inverse of the slope in order to have nonzero recruitment at equilibrium.
	steepness†	A measure of the slope of the egg–recruit relationship. Defined as the ratio of recruitment at FLEP = 0.2 and recruitment at FLEP = 1.0 (Hilborn and Walters 1992); equal to $1/(1 + 4 \times \text{CRT})$ .

Note: Entries sharing the same symbols (†, ‡, or §) are mathematically related and convey equivalent demographic information.

ture of the black rockfish (*Sebastes melanops*) population off the coast of California, estimated the value of FLEP to be 13%, and registered concern because that value was below 35%. By contrast, the most recent assessment of black rockfish stocks on the U.S. Pacific coast assumed that the stock has a CRT much lower than 35% and concluded that the stock was healthy despite consistent declines in catch per unit effort in California (Sampson 2007; Appendix A). As California begins to implement MPAs to conserve black rockfish (and other species), there is no consensus as to whether this stock is actually in need of greater protection. Here we describe a method for presenting decision makers with the range of possible management outcomes, given uncertainty in the fishery stock status of multiple species, so that spatial management decisions can account for these uncertainties in a quantitative manner.

For the purposes of MPA design, it is necessary to adapt nonspatial representations of population dynamics, such as the models used in stock assessments, to a representation that can incorporate spatial variation in fishing effort and other factors. Making this transition requires several steps. First, the density-dependent post-dispersal mortality represented by the egg–recruit relationship in stock assessments is assumed to occur within each individual model cell. The value of CRT estimated for the entire stock is then used as the slope at the origin of the settler–recruit relationship within each cell (cf. Kaplan et al. 2006, Walters et al. 2007). Second, it is necessary to represent all of the larval dispersal

pathways among model cells in order to account for all possible replacement paths (Hastings and Botsford 2006). Finally, it is necessary to specify the level of harvest (i.e., FLEP) that will occur inside and outside of MPA boundaries.

Estimation of the actual stock status that will exist outside of proposed future MPAs is complicated by several factors. First, FLEP depends on future (conventional) fishery management decisions that are both subject to change and are often made independently of MPA implementation processes (e.g., CDFG 2008). Second, future patterns of effort will depend on the fishermen’s responses to economic changes in the seascape brought about by the implementation of MPAs (e.g., Smith and Wilen 2003). Third, in addition to these uncertainties, decision makers must render judgments regarding the socioeconomic value of multiple species, each of which may have been managed separately in the past and which are likely to respond differently to MPA implementation. Moreover, it is also politically desirable to incorporate uncertainties and prior beliefs about stock status in a transparent way that is accessible to the stakeholder audience, rather than to make subtle choices of parameter values that can be buried deep within models (e.g., steepness of stock–recruitment curves; Rose and Cowan 2003).

Decision theory provides a quantitative framework for handling the uncertainties mentioned here (Peterman and Anderson 1999, Harwood and Stokes 2003, Drechsler and Burgman 2004). Decision analysis gener-

ally operates by specifying a range of possible “states of nature” (e.g., values for crucial model parameters) and the probability that each state of nature will occur, then producing model results under each state to illustrate the likely range of outcomes (Punt and Hilborn 1997, Wade 2000, Ludwig et al. 2001). This broad framework can deal with uncertainty in the underlying biology (any combination of process, observation, or model uncertainty; i.e., what is the CRT of a fish population?) as well as uncertainty about future human actions (implementation uncertainty; i.e., how much fishing will occur outside of MPAs? [Harwood and Stokes 2003, Hilborn et al. 2004]). This decision analysis approach is often used to assess uncertainty in fisheries management on the U.S. west coast.

Addressing uncertainty in fisheries management requires predictions about the probability of future human actions. However, most theoretical investigations of MPA design have simply made the precautionary assumption that harvest rates are exceedingly high relative to the persistence threshold (e.g., Botsford et al. 2001, Neubert 2003; but see alternative examples in Botsford et al. [2001]). This “scorched earth” assumption (i.e., no reproduction outside of MPAs) is useful for illustrating the performance of hypothetical MPAs under extreme conditions, but will not provide decision makers with an accurate assessment of the likely costs and benefits of real-world MPAs. The latter task requires an informed specification of the probability of different management strategies and the relative value of different fishery stocks.

In summary, the complexity and the uncertainties involved in implementation of MPAs have resulted in a wide range of viewpoints regarding their effectiveness at accomplishing conservation and fishery goals. There is a need to understand the kinds of responses that will result from MPA implementation, even though one cannot precisely predict when they will occur. Moreover, once that system behavior is understood, there is a need to formulate an approach that allows presentation of the options to decision makers in a way that incorporates the uncertainties associated with multiple species.

In this paper we have two goals: (1) to illustrate the general way in which conservation and fishery effects of MPA arrays depend on fishery management outside MPAs and (2) to formulate and illustrate a means for accounting for the uncertainties in responses of a number of different species in assessing the potential success of proposed MPA plans. First, we use a model of a theoretical, infinite coastline of continuous habitat to describe the changes in sustainability and catch that will result from increasing coverage with MPAs, over a range of assumptions regarding possible stock status and species characteristics such as movement rates. Second, we present a decision support framework for siting MPAs when future overfishing status of multiple stocks is uncertain, using a recent example from coastal California.

## METHODS

### Basic model

To maintain a common currency with stock assessments, we formulated spatially explicit population models in terms of the fundamental population parameters that determine sustainability in fishery management, FLEP and CRT. We modeled population dynamics using the dispersal-per-recruit (DPR) method described by Kaplan and colleagues (Kaplan et al. 2006, 2009, Moffitt et al. 2009), which finds equilibria more efficiently than full simulations. Briefly, the model describes a population occupying a linear coastline comprised of a variable number of discrete spatial cells. The fishing harvest rate in each cell determines the FLEP of individuals residing in that cell, ranging from the unfished state (FLEP = 1) to scorched-earth harvest (FLEP = 0).

To represent the dispersal of pelagic larvae among model cells, we assumed that eggs (and consequently, larvae) produced in each cell dispersed to neighboring cells according to a dispersal kernel (Largier 2003). We used a Gaussian dispersal kernel (Siegel et al. 2003), such that the probability of a larva dispersing from cell  $i$  to cell  $j$ ,  $D_{ij}$ , is a function of the linear distance between  $i$  and  $j$  and is given by a normal probability distribution with parameters  $\mu$  and  $\sigma$ , where  $\mu$  is the mean displacement from  $i$  (which we assume to be zero, representing a non-advective environment) and  $\sigma$  is the standard deviation of the kernel (i.e., the mean dispersal distance in one direction). If there is no suitable habitat in cell  $j$ ,  $D_{ij} = 0$ . At equilibrium, the relative density of recruits at cell  $i$  along the coast can be expressed as the sum of larval production in all other cells and the dispersal from those cells to  $i$ :

$$R_i = f(S_i)$$

$$S_i = \sum_j D_{ji} \text{FLEP}_j R_j \quad (1)$$

where  $f(S)$  is the relationship between settlers,  $S$ , and recruits,  $R$ . Equilibrium reproductive output in a cell is the product of egg production per recruit, FLEP, times recruit density,  $R$ . Because lifetime egg production is expressed as a fraction of the unfished maximum, both  $S$  and  $R$  are also scaled as fractions of their unfished maximum values.

We assume that larvae arriving at a cell experience density-dependent mortality following a Beverton-Holt recruitment function:

$$f(S) = \frac{aS}{1 + \frac{a}{b}S} \quad (2)$$

where  $a$  is density-independent survivorship, describing the slope at low settler densities, and  $b$  is the asymptotic maximum number of settlers that can survive to recruitment in each cell. We let  $b$  take the arbitrary value of 1 (this simply sets the areal units of population

density) and parameterize the slope,  $a$ , such that a population without MPAs persists when  $FLEP \geq CRT$ . This parameterization reflects the condition that a natural population will collapse when FLEP falls below CRT. If larval mortality or larval wastage (the proportion of larvae that fail to disperse to suitable habitat) are not explicitly included in the dispersal probabilities,  $D_{ij}$ , (i.e., if

$$\sum_{j=1}^n D_{ij} = 1 \tag{3}$$

so all eggs are assumed to disperse successfully) then those processes are implicitly included in the parameter  $a$  and the persistence threshold is simply  $a = 1/CRT$ . This would be the case for a nonspatial population model or in a spatially explicit model in which the coastline consists of homogeneous habitat. If the values of  $D_{ij}$  do explicitly include some larval wastage (e.g., if the habitat is heterogeneous and some larvae disperse to non-habitat cells where they die, causing the sum in Eq. 3 to fall below 1), that loss should no longer be implicitly included in  $a$ , and the value of  $a$  must be adjusted upward to ensure that the persistence threshold occurs at  $FLEP = CRT$ . This is accomplished by setting  $a = 1/(CRT \times \lambda_{\mathbf{D}})$ , where  $\lambda_{\mathbf{D}}$  is the largest eigenvalue of the dispersal matrix  $\mathbf{D}$ , which has elements  $D_{ij}$  (note that if Eq. 3 is true,  $\lambda_{\mathbf{D}} = 1$  [White 2010]). This correction relies on the assumption that at low densities (such as near the collapse point), population dynamics are approximately linear (e.g., Hastings and Botsford 2006).

The model operates by initially assuming that the habitat is fully saturated with recruits, calculating the FLEP of those recruits in each cell, then using the dispersal kernel and recruitment function to calculate the expected density of recruits in each cell given that distribution of FLEP. The process is then repeated using the new spatial distribution of recruits; this algorithm converges quickly to the equilibrium spatial distribution of recruits (Kaplan et al. 2006). From that distribution it is possible to determine which regions of space support persistent populations and to calculate the equilibrium fishery yield (based on the yield per recruit [YPR]; see next paragraph) in each location.

An advantage of casting the model in terms of FLEP is that it becomes possible to describe a generic population with a particular level of overfishing relative to the CRT as well as modeling real species with actual life history parameters. To give a typical example, consider a species with von Bertalanffy growth, age-independent post-recruitment mortality, and fecundity proportional to biomass. Length at age  $t$ ,  $L_t$ , is given by  $L_t = L_{\infty}(1 - \exp(-k[t - t_0]))$ , ( $t_0$ ,  $L_{\infty}$ , and  $k$  are von Bertalanffy growth parameters); annual mortality rate is  $m$ , and fecundity at length  $L_t$  is  $E_t = gL_t^h$  ( $g$  and  $h$  are constants). Growth is independent of population density. If annual fishing harvest rate in each cell is  $F_i$ ,

$$FLEP_i = \frac{\sum_t E_t \exp(-t(F_i + m))}{\sum_t E_t \exp(-tm)} \tag{4}$$

which is the fished LEP divided by the virgin LEP. Yield per recruit, YPR, can also be calculated, given biomass  $B_t = qL_t^p$  ( $q$  and  $p$  are constants), as

$$YPR = \frac{F_i}{F_i + m} \sum_t B_t \exp(-(t-1)(F_i + m)) \times [1 - \exp(-(F_i + m))]. \tag{5}$$

Spatial variation in the exposure to fishing is described by the value of  $FLEP_i$  associated with individuals recruiting to each cell  $i$ . Each cell has a binary classification of suitable or unsuitable habitat. Larvae cannot settle on unsuitable habitat and cells lacking habitat have  $FLEP = 0$ ; larvae settling to suitable habitat inside a no-take MPA have  $FLEP = 1$  (the unfished state). Cells containing suitable habitat outside no-take MPAs are associated with a value of FLEP that describes the intensity of fishing ( $F_i$ ) in that cell.

The levels of FLEP represented in the model were intended to describe the effects of a future fishery management policy. We were not attempting to ensure that the (unknown) present-day level of fishing effort was conserved after MPA implementation. As such, simulations with the same FLEP but a greater fraction of the coastline in MPAs have lower total fishing effort. Furthermore, we assumed that fishing effort was constant across space outside of MPAs. To determine whether model results were sensitive to this relatively simple assumption about fishing fleet dynamics, we also implemented a so-called gravity model in which fishermen allocate fishing effort according to the spatial distribution of fish biomass and fishery yield (Walters et al. 1993). This alternative approach yielded different spatial patterns of yield but did not affect the overall relationship between the total area in reserves and the persistence or yield of the fished populations, and it did not affect the ordering of proposals in the California North Central Coast example (J. W. White, *unpublished data*). Therefore we only present results from the simpler model with spatially constant effort.

Many species exhibit movement in home ranges that may carry them across MPA boundaries. Consequently, individuals settling near the edge of an MPA will only be protected from fishing in the portions of their home range that lie inside the MPA (Kellner et al. 2007, Moffitt et al. 2009). To account for this effect, we used the method developed by Moffitt et al. (2009) to model fish movement. Briefly, we assumed that new recruits establish a symmetrical home range centered on their settlement location, that each species has home ranges of a characteristic radius, and that an individual is equally likely to be found at any point within its home range at a

given time (i.e., there is a uniform spatial probability distribution of an individual's position within the home range). We then convolved the spatial distribution of home range usage with the spatial distribution of fishing effort along the coastline to determine the effective fishing rate experienced by new recruits at each location:

$$\hat{F}_i = \frac{1}{H} \sum_{j=x-(H/2)}^{x+(H/2)} c_j F_j \quad (6)$$

where  $\hat{F}_i$  is the effective fishing rate experienced by an individual with a home range centered at spatial cell  $i$ ,  $F_j$  is the fishing rate in cell  $j$ ,  $c_j = 0$  for reserves and 1 for fished areas, and  $H$  is the diameter of the home range. The effective fishing rate  $\hat{F}_i$  was then used to calculate  $FLEP_i$  and the expected fishery yield of recruits settling at each cell. We assumed that home ranges could span regions of unsuitable habitat separating cells with habitat, but that individuals did not spend time in the unsuitable portions and could not be harvested there (in such cases, the denominator of the first term on the right-hand side of Eq. 6 is reduced by the number of non-habitat cells within the home range).

#### General effects of MPAs on conservation and yield

To examine the importance of future fishery management scenarios on MPA success in a general case, we modeled a generic, one-dimensional, infinite coastline with periodic, evenly spaced no-take MPAs (cf. Botsford et al. 2001). We rendered the coastline effectively infinite by making it circular, so there were no boundaries. The repeating unit consisted of a single MPA with a length of 100 spatial units and then a stretch of fished habitat that varied in length among model runs so that the fraction of the coastline protected by MPAs ranged from 0 to 100%.

On this infinite coastline, we modeled the dynamics of two different hypothetical species, A and B. Both had long larval dispersal distances ( $\sigma = 1000$  spatial units, or 10 times the MPA width) but differed in adult movement ( $H_A = 25$  spatial units, or 25% of MPA width;  $H_B = 200$  spatial units, or twice the MPA width). We did not include the case of short-distance dispersers because as dispersal distance approaches zero, conservation benefits increase linearly with MPA area, and the effect of MPAs on fishery yield is primarily due to adult movement (Moffitt et al. 2009). For simplicity we assumed a constant CRT of 0.35 and simulated a range of fishery management conditions outside MPAs by using values of FLEP ranging from 0 (heavily overfished) to 0.6 (fishing effort approximately that which produces MSY for that CRT). Note that these values describe the FLEP realized by recruits settling outside of MPAs; recruits inside MPAs had  $FLEP = 1$  (discounted for movement outside of MPAs as described by Eq. 5). The 0.35 value for the CRT was originally used in the management of Pacific groundfishes; allowing populations to reach  $FLEP = 0.35$  led to declines to undesirable

stock levels (Ralston 2002), suggesting that the CRT is in the vicinity of that value. Model simulations using different CRT values revealed that qualitative behavior (e.g., the shape of the curve relating fishery yield to the fraction of the coastline in MPAs) depends primarily on the relative value of FLEP and CRT, not on the actual CRT value. Quantitative results, such as the minimum fraction of the coastline in MPAs required for population persistence or to maximize yield, do depend on the precise value of CRT, as illustrated by Botsford et al. (2001) and White et al. (2010).

For each species and each combination of MPA configuration (percentage of coastline protected) and fishery management (FLEP outside MPAs), we calculated the spatial distribution of settlers at equilibrium. From this result we calculated two response variables: the mean density of recruits along the coastline (a measure of conservation performance henceforth referred to as "mean recruitment") and mean fishery yield along the coastline (calculated from equilibrium recruitment and YPR). Growth parameters for black rockfish, *Sebastes melanops* (see Appendix B), were used to calculate YPR for both hypothetical species, but we then non-dimensionalized yields by estimating the MSY in a system with no MPAs and dividing all yield estimates by that value. Recruitment was similarly rescaled by dividing all values by the maximum recruit density observed in an unfished population. This rescaling facilitated comparisons among species and between this model and the species-specific California North Central Coast model.

#### California North Central Coast model

To explore the consequences of implementation uncertainty in the context of an actual conservation scenario, we applied our modeling framework to a collection of MPA packages proposed for implementation along the North Central Coast region of California, USA (see maps in Appendix C), as part of the California Marine Life Protection Act (MLPA) Initiative (CDFG 2008). We used our population dynamics model to compare recruitment and yield at equilibrium for 10 different proposed MPA networks relative to the "No Action" scenario of existing MPAs. Each proposal was developed by a group of regional stakeholders who were instructed to follow guidelines for MPA size (alongshore MPA width) and spacing (alongshore distance between MPAs) as well as other requirements such as habitat replication (CDFG 2008). The MPA networks consisted of both no-take "reserves" and "conservation areas" in which harvest of some species was to be permitted; these species-specific take regulations were included in the model.

We modeled the dynamics of six species of economic importance in the region for which biological parameters were available: black rockfish (*Sebastes melanops*), canary rockfish (*Sebastes pinniger*), cabezon (*Scorpaenichthys marmoratus*), lingcod (*Ophiodon elon-*

*gatus*), red abalone (*Haliotis rufescens*), and red sea urchin (*Strongylocentrotus franciscanus*). Demographic parameters for each species are given in Appendix B.

For simplicity we treated the California coastline as a one-dimensional spatial domain as in the idealized continuous habitat model. This was accomplished by allowing each one-dimensional spatial cell to describe the type of habitat and type of fishing allowed in one 1 km wide latitudinal strip extending offshore from the beach. In this way each one-dimensional cell can be described in terms of the distance in kilometers from the northern edge of the model domain. In addition to the North Central Coast study region, the model domain also included 100 km of the coastline to the north and south of the study region and the offshore Farallon Islands, including MPAs present in those regions (see Appendix C for details of the one-dimensional approximation). Dispersal was once again modeled using a Gaussian kernel with mean = 0 and standard deviation estimated separately for each species (see Appendix B). A Gaussian kernel is a reasonable approximation for dispersal patterns in this region of coastal California (Siegel et al. 2003) with the caveat that this kernel is intended to represent a long-term average over many spawning seasons rather than the kernel for any particular year (Siegel et al. 2008).

We modeled the dynamics of each species separately and calculated the mean recruitment (relative to the unfished maximum) and mean yield (relative to MSY) at equilibrium for each species under each proposal.

#### *Decision support framework*

In our decision analysis framework, we focused on the quantities associated with the fundamental uncertainty in fishery management: the values of FLEP and CRT. Even though these two variables determine sustainability, there is considerable uncertainty regarding their value for most of the species modeled in the California example. Formal stock assessments have not been performed for some of the species; for those that have been assessed, there remains uncertainty regarding either the current estimate of FLEP or the value of the CRT. In fact, for several of the species there is no empirical support for the CRT value used in the stock assessment. From prior research (e.g., Mangel 1998, 2000, Botsford et al. 2001) and the results of the infinite coastline model (see *Results: General effects of MPAs on conservation and yield*), we know that MPA performance depends greatly on whether FLEP is less than or greater than the CRT. Given the available data, either condition is possible for any of the California species, although the probability that  $FLEP < CRT$  varies among the species.

For the purposes of decision analysis, it is desirable to represent the probabilities of different “states of nature” occurring and what the outcome of different management decisions would be given each state of nature. It is then possible to assess the probability of different outcomes and their relative costs and benefits (Hilborn

and Walters 1992, Punt and Hilborn 1997, Peterman and Anderson 1999). In this case, the different potential values of the CRT represent different states of nature for each species and alternative MPA proposals represent management options. If the decision makers tasked with MPA design are not able to influence conventional fisheries management, then the probabilities of different levels of success in conventional management (i.e., the value of FLEP) will be more like states of nature rather than additional management options. This was the case in the California example, and this situation is likely to arise anytime the jurisdiction or management body implementing MPAs differs from that implementing conventional management. Therefore we estimated the joint probability of each combination of the state of nature (CRT) and conventional management action (FLEP) occurring in the future for each of the modeled species. Estimating these probabilities is a potentially subjective undertaking and within an actual management decision process, this step would ideally involve debate and discussion among experts and decision makers (e.g., Smith et al. 2007).

For the purposes of illustration in this paper, we constructed two alternative sets of probabilities: an optimistic scenario in which stocks are assumed to be managed conservatively (i.e., greater weight is placed on lower values of CRT and higher values of FLEP) and a pessimistic scenario in which conventional management is less successful (i.e., greater weight is placed on higher CRTs and lower FLEPs). The estimates of FLEP and CRT in the pessimistic scenario were generated using the precautionary philosophy outlined by Smith et al. (2007), such that greater weight was placed on higher (more conservative) values of CRT when there was greater uncertainty about stock status. We used these probabilities to weight the model results for each species to obtain an overall estimate of mean recruitment and mean fishery yield under each future management scenario.

While it is also possible to handle uncertainty regarding states of nature by using Monte Carlo techniques to integrate over a prior distribution of alternative states (e.g., Halpern et al. 2006), we suggest that presenting the probabilities in a decision table and implementing them as post hoc weights has two advantages. First, it makes key model assumptions more transparent to non-specialists, thus reducing the potential for unreasonable probability distributions being used to bias model results (Dennis 1996); second, it forces decision makers to confront uncertainties and quantify their beliefs (Drechsler and Burgman 2004).

We obtained potential values for CRT and FLEP from stock assessments and other literature (Appendix A). We used current estimates of FLEP to represent potential future values of FLEP and generated the probabilities for the pessimistic scenario based on the recent management history of each species, using the assumption that contemporary management success can predict future efforts (Appendix A). This is a reasonable assumption in

TABLE 2. Values of fraction of lifetime egg production (FLEP) and critical replacement threshold (CRT) used in the California North Central Coast model and weightings applied to each FLEP–CRT combination for the pessimistic and optimistic management scenarios.

Species	CRT	FLEP	FLEP/CRT	Optimistic weighting	Pessimistic weighting
Abalone	0.35	0.2	0.57†	0	0.25
	0.35	0.3	0.86‡	0	0.25
	0.35	0.4	1.14§	1	0.5
Red sea urchin	0.35	0.2	0.57†	0	0.5
	0.15	0.2	1.33§	1	0.5
Black rockfish	0.35	0.13	0.37†	0	0.33
	0.16	0.13	0.81	0	0.33
	0.11	0.13	1.18‡	0	0.33
	0.35	0.7	2.00	0.33	0
	0.16	0.7	4.38	0.33	0
	0.11	0.7	6.36§	0.33	0
Cabezon	0.35	0.3	0.86†	0	0.75
	0.35	0.4	1.14‡	0	0.25
	0.11	0.3	2.72	0.5	0
Canary rockfish	0.11	0.4	3.64§	0.5	0
	0.51	0.1	0.20†	0	0.25
	0.51	0.9	1.76§	1	0.75
Lingcod	0.35	0.24	0.69†	0	0.75
	0.03	0.24	8.00§	1	0.25

Notes: The alternative values of CRT represent different possible states of nature, while the alternative values of FLEP represent different possible outcomes of conventional fishery management, which we assume cannot be affected by the decision makers considering alternative marine protected area (MPA) proposals. The value FLEP/CRT is an index of the level of sustainability in the absence of MPAs; values < 1 represent overfishing. See Appendix A for explanation of values chosen for each species. Simulations marked with †, ‡, or § are shown as examples in Figs. 3–5 as the FLEP < CRT, FLEP ≈ CRT, and FLEP > CRT cases, respectively.

the sense that both current and future management success depends on the CRT (and how well we are able to estimate its value) as well as the sociopolitical pressures associated with restricting effort in a fishery.

We generated model results for each MPA proposal under each combination of FLEP and CRT for each of the six species. We then aggregated the results for each proposal as weighted means in two sequential steps. First, we obtained the mean recruitment and yield for each species by taking a weighted mean across each combination of FLEP and CRT. We generated two sets of weighted means for each species by using the probabilities associated with each of the two future management scenarios (optimistic and pessimistic; Table 2) as weights. Second, from these weighted means for each species, we obtained the overall mean recruitment and yield across all species for each proposal under each management scenario. These mean recruitments and yields were each calculated in two ways: an unweighted grand mean of species means (from step 1) and a weighted grand mean across species, weighted by the total commercial landings for that species within the study region in 2000–2006 (California Department of Fish and Game, *available online*).<sup>4</sup> The latter approach represents an attempt to estimate the relative economic value of each species, although we note that future economic values can be highly unpredictable. We then had a total of four estimates of mean recruitment and yield for each MPA

proposal: two future management scenarios (optimistic and pessimistic) × two methods of weighting species (unweighted and weighted by economic value), which we interpreted as alternative estimates of the expected performance of that proposal. Given these estimates, policy makers could specify a loss function describing the cost of failing to meet various conservation or economic targets, and the best MPA proposal would be associated with the minimum value of the loss function (Wade 2000). For the purpose of illustration in the absence of policy maker input, we chose an arbitrary loss function that has a value of 0 (acceptable) if the expected mean recruitment and mean yield are both greater than 50% and a value of 1 (unacceptable) otherwise. Note that in these model runs we explicitly consider uncertainty in FLEP and CRT but not in the other demographic parameters given in Appendix B. This is because FLEP effectively depends on the values of those other parameters (e.g., lifetime egg production depends on the natural mortality rate and size–fecundity relationship). Therefore it is not sensible to vary those demographic parameters independently of FLEP; moreover, variation in FLEP across model runs can be interpreted as reflecting uncertainty in those model parameters themselves as well as in fishery management (i.e., *F*).

RESULTS

*General effects of MPAs on conservation and yield*

The results from the idealized continuous habitat model, displayed as the equilibrium values of mean

<sup>4</sup> (<http://www.dfg.ca.gov/marine/fishing.asp>)



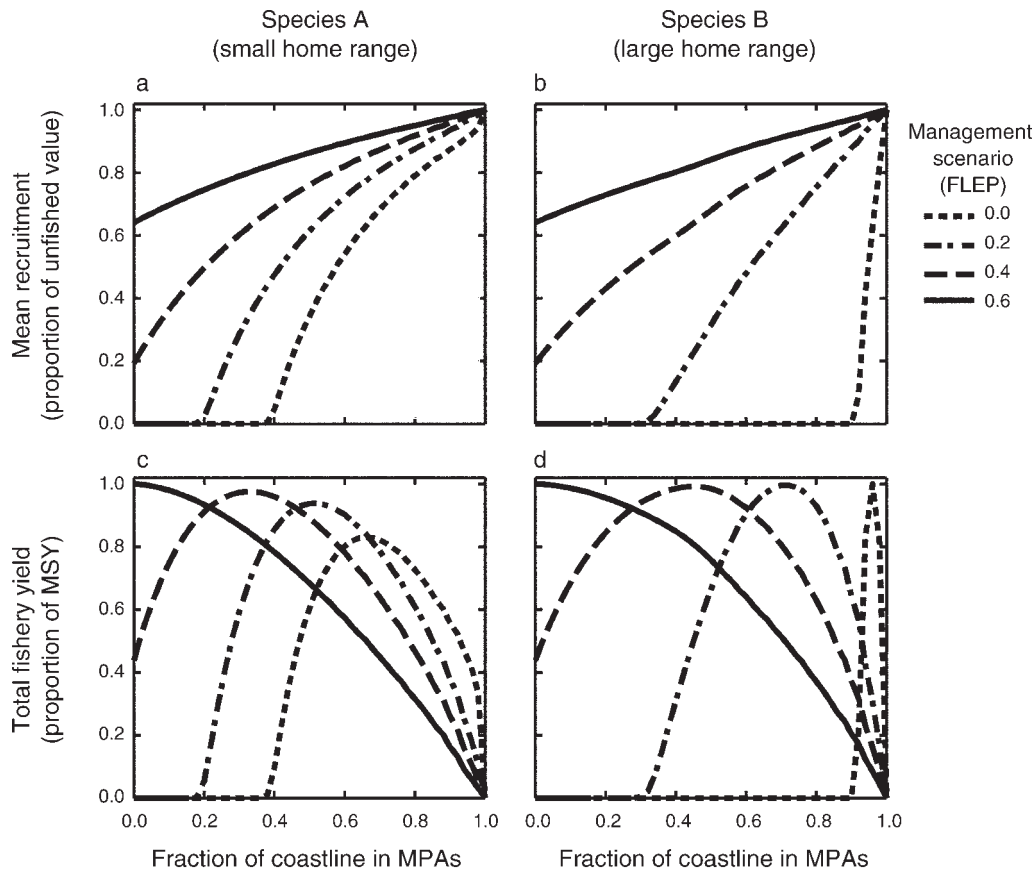


FIG. 1. Performance of two hypothetical species under different levels of fishery management success and a range of marine protected area (MPA) configurations. MPA width is constant across all scenarios. (a, c) Species A has home range diameter  $0.25 \times$  MPA width; (b, d) species B has home range diameter  $2 \times$  MPA width. Both species have mean larval dispersal of  $10 \times$  MPA width. Management success is expressed in terms of FLEP, the fraction of unfished lifetime egg production realized by recruits outside MPAs. FLEP values less than the 0.35 critical replacement threshold would be overfished in the absence of MPAs for nonmobile species. For clarity, only four levels of FLEP are shown; these are representative of the three additional scenarios (FLEP = 0.1, 0.3, 0.5) that were modeled but not shown here. The abbreviation MSY stands for maximum sustainable yield.

recruitment (as a proportion of the unfished maximum) and fishery yield (as a proportion of MSY) across the entire coastline for each species (Fig. 1), exhibit related general patterns in conservation and yield. With regard to conservation, when FLEP was less than the 35% CRT (i.e., when the stock was overfished), the stock was not persistent (recruitment = 0 and yield = 0) unless MPAs covered some minimum fraction of the coastline (bottom left corner of Fig. 1a, b). Beyond this threshold, relative recruitment increased to a maximum of 1.0 as the fraction of the coastline placed in MPAs increased. If the stock was not overfished (FLEP > 0.35), the population was persistent (recruitment > 0) regardless of MPA configuration and recruitment once again increased to 1.0 with the fraction of the coastline in MPAs. The general pattern exhibited by yield was a unimodal function of MPA coverage. There was no yield if the population was not persistent or if the entire coastline was in MPAs. Between these two extremes, yield was maximized (for a given value of FLEP) when MPAs covered a fraction of the coastline roughly

equidistant between the persistence threshold in Fig. 1a or Fig. 1b and 100% coverage. The obvious exception is FLEP values for which the population was persistent with 0% of the coastline in MPAs, where the maximum yield occurred closer to 0% of the coastline in MPAs and yield declined as the area in MPAs increased (Fig. 1c, d).

Fig. 1 also provides some information on the sensitivity of our results to our choice of 0.35 as the CRT. Note that for the small home range case (Fig. 1a), the fraction of coastline at which the species begins to persist is approximately  $(0.35 - \text{FLEP})$ . Thus if we had chosen a smaller (or larger) value of CRT, species would begin to persist at points to the left (or right) of the current ones.

The fraction of the coastline that must be in MPAs to ensure persistence and maximize yield is clearly a key model result (cf. Mangel 1998, 2000, Botsford et al. 2001), and this value is likely to be a target for policy makers. However, the location of this optimal value was strongly dependent upon the management status (i.e., FLEP value) outside MPAs. At one extreme, if

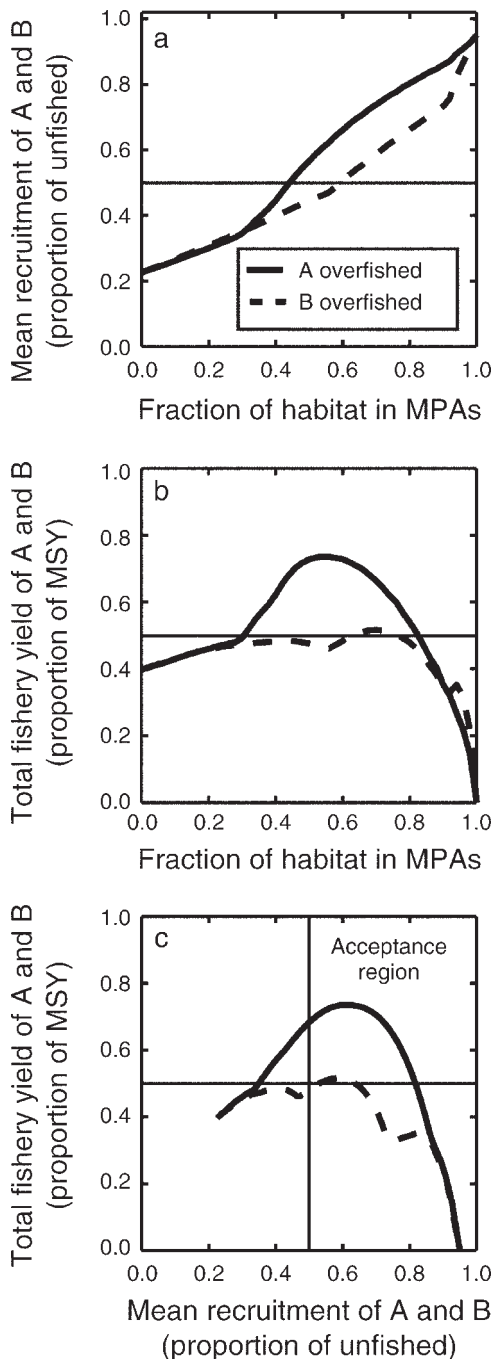


FIG. 2. Performance of different marine protected area (MPA) configurations under two different future fishery management scenarios for the two hypothetical species shown in Fig. 1. In the first scenario, species A is likely to be overfished, but species B is not (solid curve); in the second scenario, species B is likely to be overfished, but species A is not (dashed curve). Curves represent the unweighted mean performance across both species for a given scenario in terms of (a, c) recruitment or (b, c) fishery yield. Horizontal and vertical black lines indicate 50% threshold used in decision analysis loss function. Only MPA configurations within the box in the upper right-hand corner of panel (c) are acceptable according to this criterion. (a, c) Species A has home range diameter  $0.25 \times$  MPA

conventional management was sufficiently conservative, MPAs did not improve yield at all (note curve for FLEP = 0.6 in Fig. 1). The costs of misjudging a target value of fraction of coastline in reserves were asymmetrical: erring on the side of too little MPA area led to a complete loss of both yield and ecological function if there were too few MPAs to maintain a persistent population, while erring on the side of too much MPA area led to additional benefits in ecological function (increasing recruitment) but a gradual increase in economic costs (decreasing yields).

This situation poses a decision-making problem that is further compounded by the dependence of the threshold on species-specific dispersal parameters: only by great coincidence will one reserve configuration ensure persistence and maximize yield for multiple species. In this case, for any given FLEP, yield of the more sedentary species A (home range =  $0.25 \times$  MPA width) was maximized with many fewer MPAs (Fig. 1c) than yield of the more mobile species B (home range =  $2 \times$  MPA width; Fig. 1d) because MPAs of a given size are less effective in protecting fish that range beyond their boundaries (Moffitt et al. 2009).

To illustrate the management dilemma produced by this situation, we considered a simple decision analysis problem using the two hypothetical species on the infinite coastline. We modeled two different future fishery management scenarios: one in which species A (with a small home range) was likely to be overfished but species B (with a large home range) was not and a second one in which B was likely to be overfished but A was not. We assumed that there was only one possible state of nature ( $CRT = 0.35$ ) and the different management actions (the value of FLEP outside MPA boundaries) had different probabilities, depending on the future fishery scenario. The probability weights associated with overfishing were 0.3 and 0.4 for FLEP = 0.0 and 0.1, respectively, and 0.05 each for FLEP = 0.2, 0.3, 0.4, 0.5, and 0.6. The weights for non-overfishing were 0.4 and 0.3 for FLEP = 0.5 and 0.6, respectively, and 0.05 for each of the other five FLEP values. For each of the two future fishery management scenarios, we calculated mean recruitment and mean yield as the unweighted means across both species (Fig. 2).

In this theoretical scenario, the effects of MPA placement depended heavily on the relative effectiveness of management outside MPAs (cf. similar results in Holland and Brazee 1996, Mangel 1998, 2000, Sladek-Nowlis and Roberts 1999, Botsford et al. 2001). When species A was overfished but species B was not, mean recruitment of both species increased monotonically with the fraction of coastline in MPAs (Fig. 2a) and

← width; (b, d) species B has home range diameter  $2 \times$  MPA width. Both species have mean larval dispersal of  $10 \times$  MPA width. The abbreviation MSY stands for maximum sustainable yield.

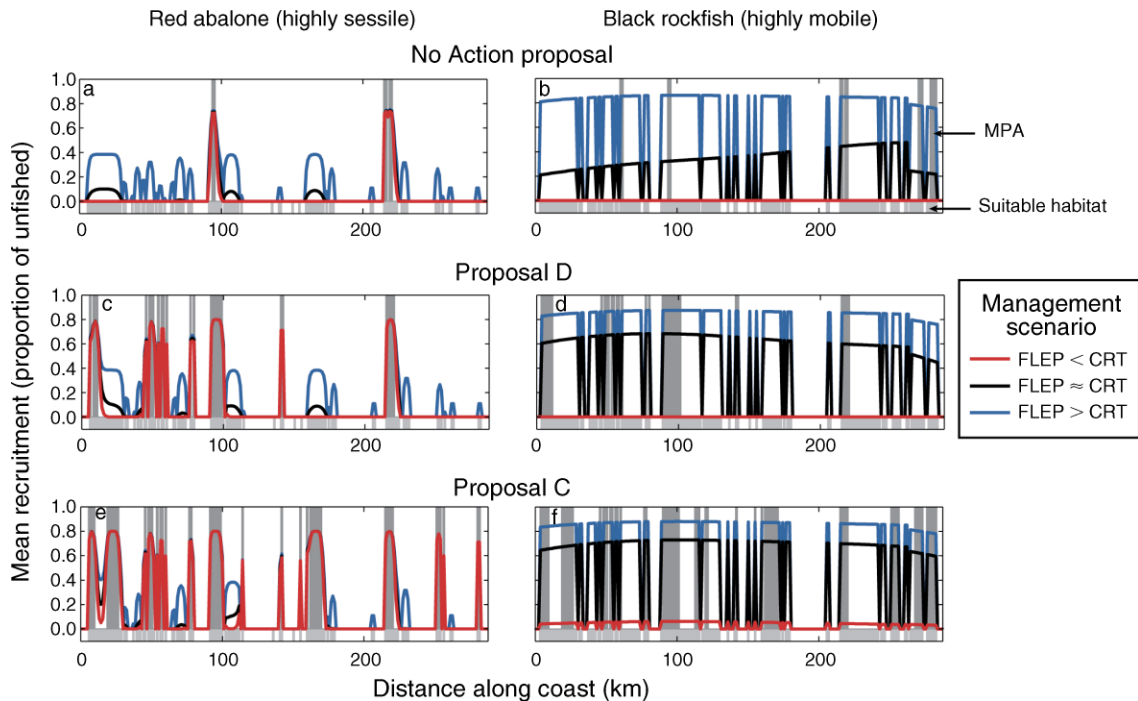


FIG. 3. Equilibrium spatial distributions of recruitment predicted for (a, c, e) red abalone (*Haliotis rufescens*) and (b, d, f) black rockfish (*Sebastes melanops*) for three representative California North Central Coast marine protected area (MPA) proposals. Light gray bars at the bottom of each graph indicate the presence of suitable habitat in one-dimensional space; dark gray bars in the background of the graph indicate the presence of MPAs (see Appendix C for details on one-dimensional representation of the California coastline). Curves indicate equilibrium recruit densities (relative to the maximum density in a habitat cell) when conventional management outside reserves leads to FLEP < CRT (overfishing, red line), FLEP  $\approx$  CRT (fishing either just below or just above persistence threshold, black line), and FLEP > CRT (not overfishing, blue line). The specific values of FLEP and CRT used for each species are given in Table 2. Note that recruitment is constrained to be zero in locations lacking suitable habitat. Maps of MPA proposals (a, b) “No Action,” (c, d) “D,” and (e, f) “C” are shown in Appendix C. Abbreviations are: FLEP, fraction of unfished lifetime egg production; CRT, critical replacement threshold.

mean yield of both species peaked at  $\sim 50\%$  of the coastline in MPAs (Fig. 2b). When B was overfished and A was not, mean recruitment was generally lower than in the first scenario for most MPA configurations (Fig. 2a), and yield peaked at a much higher fraction of the coastline in MPAs (Fig. 2b). Applying the 50% loss function (indicated by the horizontal and vertical lines in Fig. 2), a broad range of MPA configurations were acceptable when species A was overfished, but only configurations with  $\sim 70\%$  of the coastline in MPAs met the 50% threshold when B was overfished (Fig. 2c).

Thus, policy decisions in this scenario would be highly sensitive to projections regarding the future success of conventional management for these two species. Managers seeking to conserve both species would have to restrict fishing over most of the coastline given one possible outcome (B is overfished, A is not) but could achieve the same result with many fewer MPAs given another possible outcome (A is overfished, B is not). The observation that there is greater benefit from the MPAs when the short-distance species is overfished is consistent with our knowledge that MPAs generally have a more reliable effect on the persistence of short-distance dispersers (Kaplan et al. 2009, Moffitt et al. 2009).

#### California North Central Coast model

The results for the model of the North Central Coast study region displayed considerable interspecific variability in the response to MPA implementation. To illustrate this variability, we present the equilibrium spatial distribution of recruits predicted by the model for red abalone and black rockfish for three representative MPA proposals and three states of nature corresponding to FLEP less than, greater than, and approximately equal to CRT (Fig. 3). Red abalone have negligible larval dispersal and home range movement and could sustain persistent subpopulations in very small MPAs, even with FLEP < CRT outside MPA boundaries (Fig. 3a). Conversely, there was very little larval spillover from within MPAs to habitat outside of MPAs. As such, when management led to a high level of fishing relative to the replacement threshold (FLEP < CRT and FLEP  $\approx$  CRT), proposals with more and/or larger MPAs supported red abalone populations within MPA boundaries but not in unprotected habitat (Fig. 3c, e), and mean recruitment increased with MPA area. By contrast, black rockfish were modeled with considerable larval dispersal (mean distance = 73 km) and adult

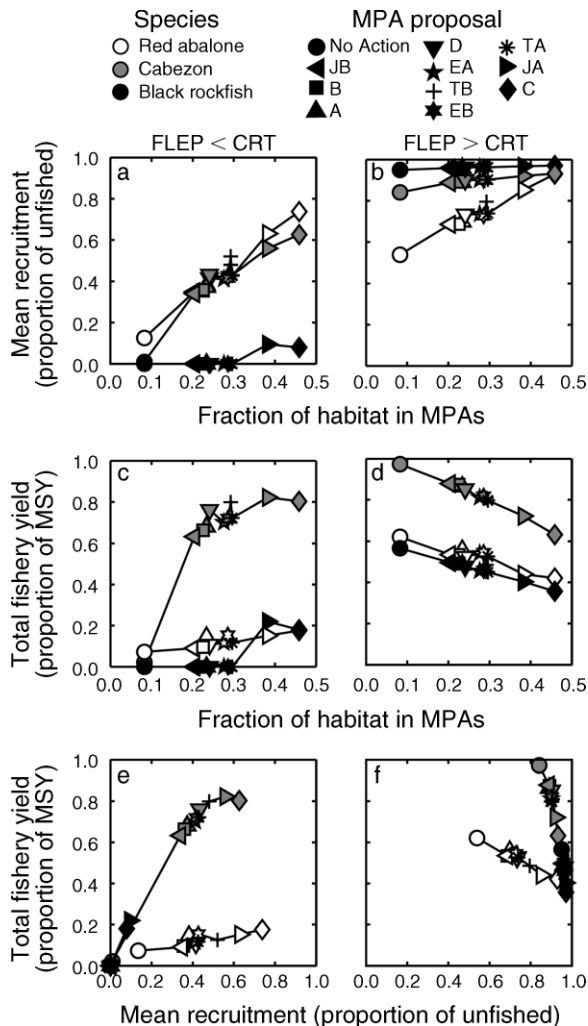


FIG. 4. Performance of California North Central Coast marine protected area (MPA) proposals for three representative species under two different potential states of nature. Symbol shapes distinguish the different proposals; fill shade indicates the species (key shows fill for rockfish). Panels (a–d) are measures of performance vs. the proportion of hard-bottom habitat in MPAs, and panels (e–f) are “phase plots” of those two measures, omitting the coverage variable. Each point is the (a–b) mean recruitment or (c–f) fishery yield for one species under each proposal. Proposals are ordered along the horizontal axis in panels (a–f) by the fraction of total hard-bottom habitat placed in MPAs. Results are shown for cases in which  $FLEP < CRT$  (overfishing; a, c, e) or  $FLEP > CRT$  (no overfishing; b, d, f); the specific values of  $CRT$  and  $FLEP$  used for each species are given in Table 2. Abbreviations are:  $FLEP$ , fraction of unfished lifetime egg production;  $CRT$ , critical replacement threshold;  $MSY$ , maximum sustainable yield.

movement (home range diameter = 9 km) and thus received less benefit from smaller MPAs. With  $FLEP < CRT$ , the black rockfish population did not persist in the No Action proposal (Fig. 3b), but was persistent under proposals with more area in MPAs (Fig. 3f). Mean recruitment increased with MPA area, though less

dramatically, for higher values of  $FLEP$  relative to  $CRT$  (Fig. 3b, d, f).

We summarized the results for each species as the mean recruitment and yield (over the entire coastline) for a particular MPA proposal and state of nature ( $FLEP$  and  $CRT$  values). Several representative examples of these results are shown in Fig. 4. These plots are similar to those for the continuous habitat model (Fig. 1) in that they summarize the costs and benefits of increasing MPA area and further reveal the interspecific variability in MPA effects. The series of points for each species in Fig. 4 is essentially analogous to segments of the curves shown in Fig. 1. That is, Fig. 4a corresponds to the curves for  $FLEP = 0.0$  or  $0.2$  in Fig. 1a, b (mean recruitment for  $FLEP < CRT$ ), Fig. 4b corresponds to  $FLEP = 0.4$  or  $0.6$  in Fig. 1a, b (mean recruitment for  $FLEP > CRT$ ); Fig. 4c and d similarly correspond to the curves for  $FLEP < CRT$  and  $FLEP > CRT$ , respectively, in Fig. 1c, d (fishery yield). In general, species with smaller adult home ranges (e.g., red abalone, cabezon) were better protected by a given MPA proposal, with higher mean recruitment and yield than species with larger home ranges (e.g., note that for  $FLEP < CRT$ , black rockfish remained at zero recruitment until the fraction of coastline in MPAs exceeded 0.35). Despite this interspecific variability, results tended to mirror those from the continuous habitat model (Fig. 1): when  $FLEP < CRT$ , some minimum area in MPAs is required to sustain persistent populations and obtain fishery yield; beyond this threshold, recruitment increases monotonically to a maximum while yield increases to a maximum then decreases as additional MPA area is added (Fig. 4a, c, e). When  $FLEP > CRT$ , recruitment still increases with MPA area, but yield declines monotonically.

We further summarized the predicted effects of MPA implementation on the entire suite of species by taking the unweighted mean of both recruitment and yield across all species for each MPA proposal and three representative states of nature:  $FLEP < CRT$ ,  $FLEP \approx CRT$ , and  $FLEP > CRT$  (Fig. 5; the values of  $FLEP$  and  $CRT$  used for each species in each panel are indicated in Table 2). This summary highlights the overall trend in the effect of MPAs: when species were overfished (or nearly so) outside of MPAs ( $FLEP < CRT$  and  $FLEP \approx CRT$ ), both mean recruitment and yield tended to increase with MPA area. However, when conventional management was more conservative ( $FLEP > CRT$ ), there was a trade-off: recruitment increases but yield decreases with increasing MPA area (Fig. 5c).

As might be expected from the large differences due to different values of  $FLEP$  in Fig. 1, the two alternative future fishery management scenarios for each species (Table 2) led to very different mean estimates of MPA performance (Fig. 6). Whereas Fig. 5 presents model results as an unweighted mean across all species for each state of nature, Fig. 6 displays the same data weighted in four different ways: two alternative weighted means

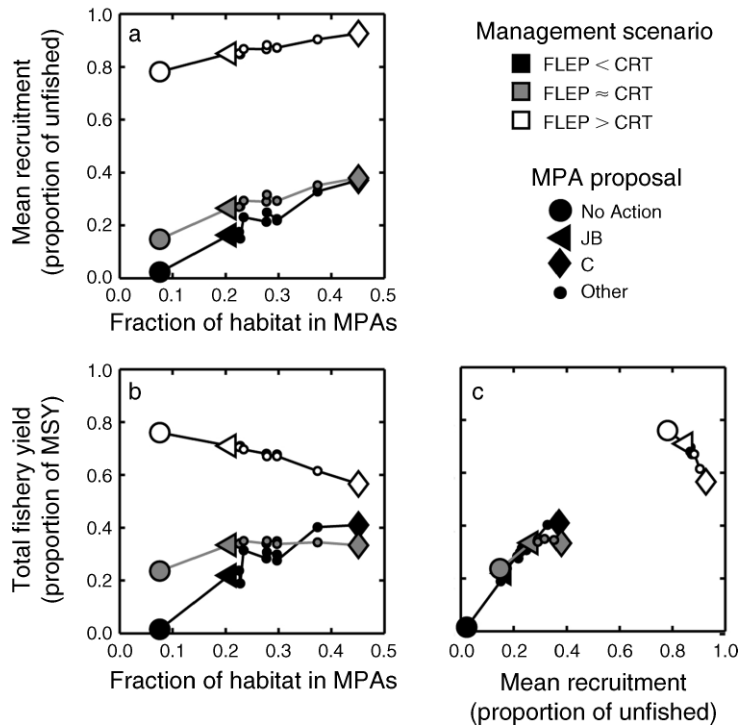


FIG. 5. Performance of the 11 California North Central Coast marine protected area (MPA) proposals for six species under three potential states of nature. Symbol shapes distinguish the different proposals; fill shade indicates the management scenario. (a, b) Measures of performance vs. the proportion of hard-bottom habitat in MPAs and (c) a “phase plot” of those two measures, omitting the coverage variable. Each point is the (a, c) mean recruitment or (b, c) fishery yield for all six species under each proposal. Results are shown for cases in which  $FLEP < CRT$  (overfishing),  $FLEP \approx CRT$  (fishing near the persistence threshold), or  $FLEP > CRT$  (not overfishing); the specific values of CRT and FLEP used for each species are given in Table 2. For clarity, only selected proposals are identified by name. Abbreviations are: FLEP, fraction of unfished lifetime egg production; CRT, critical replacement threshold; MSY, maximum sustainable yield.

across states of nature (representing either pessimistic or optimistic projections for future management success) and two alternative weighted means across species (either unweighted or based on contemporary commercial landings). The goal of this analysis was to determine the costs and benefits of implementing each MPA proposal, relative to the No Action alternative, and also to identify the proposals that would produce the most desirable outcomes given the pre-specified loss function. For clarity, not every proposal is shown with a unique symbol in Figs. 5 and 6; only a few key examples are specifically identified.

The optimistic management scenario assigned high probabilities to cases in which  $FLEP > CRT$  (Table 2), which led to the prediction that all proposals had relatively high recruitment and that yield declined with increasing MPA area (symbols with dotted outlines in Fig. 6a, b). Regardless of species weightings, the arbitrary 50% loss function indicated that all MPA configurations were acceptable, including No Action (all data points with dotted outlines lie in the upper right quadrant of Fig. 6c). Proposal C had the highest recruitment (it had the most area in MPAs of any proposal) and the highest yield was found in either the

No Action proposal (unweighted mean) or Proposal JB (species weighted by value; both proposals had relatively little area in MPAs). Strikingly different results were obtained under the pessimistic fishery management scenario (Table 2). Under that scenario, which placed greater weight on cases for which  $FLEP < CRT$ , recruitment once again tended to increase with MPA area (indeed, several species were not expected to persist under the No Action proposal), but yields were maximized, rather than minimized, under proposals with the greatest amount of area in MPAs (symbols with solid outlines in Fig. 6a, b). When species were weighted evenly, the loss function identified proposals C and JA as the best options (note two open symbols with solid outlines in the upper right quadrant of Fig. 6c); proposals D, EB, and TB were also within the acceptable region. When species were weighted by economic value, those proposals, as well as C, JA, and TA, were acceptable (note the shaded symbols with the solid outline in upper right quadrant of Fig. 6c). The two alternative scenarios led to nearly opposite posterior estimates of the “best” MPA alternative: under the optimistic scenario, proposal C was the worst alternative in terms of fishery yield, while that proposal was one of

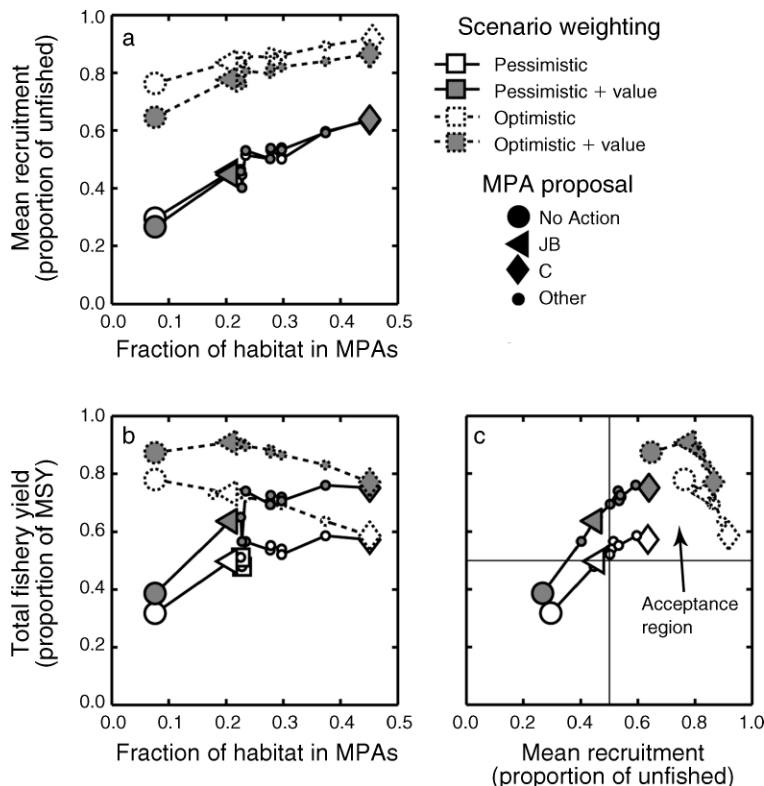


FIG. 6. Performance of California North Central Coast marine protected area (MPA) proposals for six species under two different future fishery management scenarios and two methods for species valuation. Symbol shapes distinguish the different proposals. Results for each species were weighted by the probability of that species having a particular combination of the critical replacement threshold (CRT) and fraction of lifetime egg production (FLEP), based on either an optimistic (symbols with dotted outlines) or pessimistic (symbols with solid outlines) projection of future fishery management success. Results for each species were then combined with an unweighted mean (open symbols) or a mean weighted by the commercial value of the stock (shaded symbols). Each point is the (a, c) mean recruitment or (b, c) fishery yield for all seven species under each proposal. Proposals are ordered by the fraction of total hard-bottom habitat placed in MPAs in panels (a) and (b). Horizontal and vertical black lines in panel (c) indicate 50% threshold used in decision analysis loss function. Only MPA configurations within the box in the upper right-hand corner of panel (c) are acceptable according to this criterion. For clarity, only selected proposals are identified by name. The abbreviation MSY stands for maximum sustainable yield.

only a few with acceptable levels of yield in the pessimistic scenario.

DISCUSSION

The decision making process described here has illuminated the practical difficulties presented by known, but not widely appreciated, results. It is well established that MPAs can sustain fisheries that would otherwise collapse due to overharvesting (Botsford et al. 2001, Gaylord et al. 2005, White and Kendall 2007). The converse of this finding, that MPAs potentially offer little benefit to well-managed fisheries (Botsford et al. 2003), seems obvious, but few envision the consequence shown here: a decline in yield with increasing MPA area illustrated in Figs. 4d, 5b, and 6b. This equivalence between spatial and conventional management is a fundamental property of any model of an exploited population, from analytical, nonspatial approaches (Holland and Brazee 1996, Guénette and Pitcher 1999, Hastings and Botsford 1999, Sladek-Nowlis and

Roberts 1999, Mangel 2000, White and Kendall 2007, Ralston and O’Farrell 2008) to complex, spatially explicit models (Gaylord et al. 2005). However, a poorly appreciated consequence of this equivalence is that it causes decision making for actual MPA implementation to be extremely complex, especially when contending with multiple species with poorly known movement parameters and persistence characteristics. For each species, low area in MPAs may not produce any yield, then yield might increase as area increases, but then it begins to decline as more area is put into MPAs, and the break points will differ among species.

In an ideal world, MPA configurations and conventional fishery regulations could be tailored to optimize harvest and profit for each individual fishery (Sanchiricho et al. 2006, White et al. 2008). In the real world, interspecific variability and a host of uncertainties regarding biology and future human behavior stand in the way of such optimization. Applications of decision theory to fishery management and MPA design

have generally focused on uncertainty regarding biological parameters (Punt and Hilborn 1997, Hill et al. 2007). For example, Halpern et al. (2006) used a decision analysis approach to formulate MPA spacing recommendations given uncertainty in the shape and width of larval dispersal kernels, and Gerber et al. (2007) generated decision rules for MPA implementation that account for the quality of monitoring data. Fewer investigators of MPA efficacy have addressed the problem of uncertainty in future fisheries management strategies (Mangel 2000), but our models revealed that MPA implementation is also highly sensitive to this type of uncertainty, and we described a decision support approach to better grapple with it.

Given the equivalence between MPAs and conventional management (Mangel 1998, 2000, Hastings and Botsford 1999), it is perhaps not surprising that the dome-like shape of the plot of fishery yield vs. the fraction of coastline in MPAs (Fig. 1c, d) is similar to the plot of fishery yield vs. fishing effort under a conventional management regime flipped about the yield axis (Fig. 7). In Fig. 7 we show the expected yield over a range of harvest rates ( $F$ ) from a spatially implicit population model of black rockfish with the same egg-recruit curve used in the spatially explicit California model. In this example we have specified fishing effort, so uncertainty regarding stock status is represented by showing the results for a range of values of the CRT. As  $F$  increases from left to right in Fig. 7, FLEP declines. Just as yield increases but then collapses when total MPA area is decreased (Fig. 1c, d), yield increases to a maximum (MSY) with increased fishing effort before the population is driven to collapse.

Comparison of Figs. 1 and 7 is a way to compare the decision-making problems of MPA implementation and conventional fishery management. Each species in the system of MPAs in Fig. 1c, d would correspond to one curve in Fig. 7, although it would be difficult to know which curve due to uncertainty regarding CRT. The major difference between the two decision processes is that in the case of conventional fishery management, attention can be focused on a single species (though not always completely independently), while MPAs apply the same set of regulations on all species simultaneously.

The results of the infinite coastline model illustrate three of the major problems facing MPA planners. First, the success of any MPA proposal, especially one protecting a relatively small fraction of the coastline, depends heavily on the management outside MPA boundaries (cf. Holland and Brazee 1996, Botsford et al. 2001, Kaplan et al. 2006, 2009). Second, for any given management policy, there is a complex relationship between MPA area and fishery yield: MPAs must cover enough coastline to allow population persistence, but additional area beyond the persistence threshold removes fishing grounds and has an economic cost (Fig. 1c, d). Decision makers seeking to minimize the cost of lost fishery yield may attempt to approach the persis-

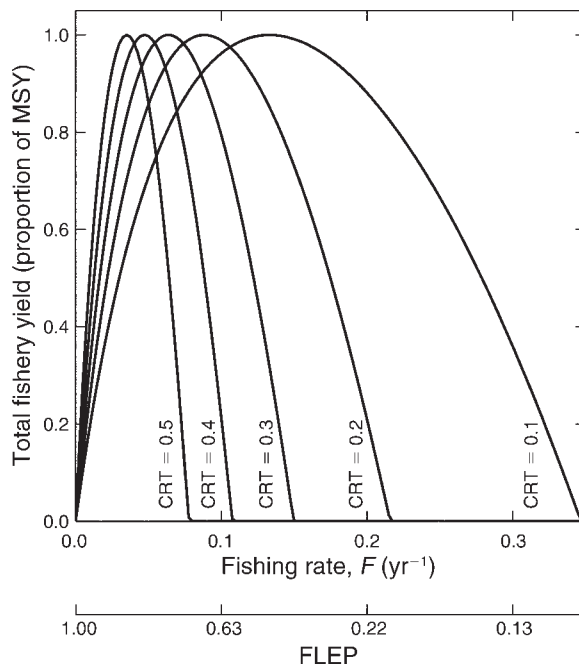


Fig. 7. Fishery yield (relative to maximum sustainable yield, MSY) for a black rockfish fishery under conventional management. Each curve shows equilibrium yield as a function of instantaneous fishing mortality rate ( $F$ ) for a population with a different critical replacement threshold (CRT). The lower horizontal axis shows the fraction of natural, unfished lifetime egg production (FLEP) for the corresponding fishing rate (note that FLEP is a nonlinear function of  $F$ ).

tence threshold as closely as possible from the right-hand side. This could lead to a situation akin to the “ratchet effect” in conventional fisheries (Botsford et al. 1997): so long as the fishery had not yet collapsed, there would be pressure from harvesters to increase harvest rates or remove MPAs until managers unwittingly crossed the persistence threshold. This familiar quandary is complicated by a third major problem to which we have already alluded: MPAs affect multiple species with vastly different life histories, and the same MPA configuration cannot ensure persistence and maximize yield for all of them (Fig. 2). The decision support framework we described for the California Coast was an attempt to handle all three of these problems.

Our method of weighting model results according to the probability of different states of nature and/or conventional management success under different future fishery management scenarios presents policy makers with the essential elements of the MPA decision process: the size, spacing, and location of proposed MPAs within the habitat, the effect of fishing on population dynamics and replacement (represented by FLEP), and the level of replacement required for a sustainable population (i.e., CRT). This presents a more comprehensive picture of the decision structure than earlier, more strategic results, founded on idealized assumptions such as no egg

production outside MPAs (i.e., “scorched earth”). Harvest rates are unlikely to reach such extremes (White et al. 2008), so such models have a tendency to overestimate the conservation benefits of MPAs while underestimating their potential costs to otherwise well-managed fisheries. Our method provides a more complete analysis than merely adhering to size and spacing guidelines (Halpern et al. 2006; E. A. Moffitt, J. W. White, and L. W. Botsford, *unpublished manuscript*), as is also done in the California MLPA process (CDFG 2008). It also affords some advantages over similar tactical approaches (e.g., Little et al. 2007, Walters et al. 2007) in which models were parameterized using estimates of the stock–recruitment relationship drawn from stock assessments, then presented results in terms of values of fishing mortality,  $F$ . Although such models may incorporate realistic harvest rates, the effects of those harvest rates on population persistence will depend on the empirical estimate of the stock–recruitment relationship, the parameterization of which is fraught with uncertainty (Needle 2002, Rose and Cowan 2003). An advantage of the FLEP-based framework we used is that harvest rates are specified relative to the CRT. Thus the decision analysis captures uncertainty in both the harvest rate (how much fishing will there be?) and in the CRT (how much fishing can the stock support?). The qualitative results described here for overfished (FLEP < CRT) vs. underfished (FLEP > CRT) scenarios in the generic infinite coastline model would not change with a different value of CRT, but the MPA coverage required for population persistence would differ. In general, lower CRT values require less spatial coverage by MPAs for a particular value of FLEP (Botsford et al. 2001, White et al. 2010).

As with any decision support effort, our results were highly sensitive to the different probabilities associated with alternative future scenarios. Indeed, the pessimistic and optimistic fishery scenarios produced opposing recommendations for the best MPA proposal. Our intent here was not to demonstrate that one of those scenarios is closer to the truth for the California example, but rather to demonstrate the effects of making such projections about the future explicit and transparent. The difference in outcomes actually showcases the benefit of our approach. Requiring decision makers to specify the probability they assign to different states of nature (CRTs) or future conventional management outcomes (FLEPs) makes crucial modeling assumptions far more transparent to stakeholders and other observers, rather than allowing those assumptions to be buried within the model itself. This added transparency should help prevent unscrupulous stakeholders or modelers from “gaming” the probability distributions to favor a desired outcome (Dennis 1996).

The decision analysis presented here is not intended to be a definitive answer to the question of MPA design. The complexity, subjectivity, and variability of the analysis indicate the need for further work to integrate

better the management of conventional fisheries and MPAs (cf. Botsford et al. 2008). The decisions to be made here are complicated by the differences between spatial and nonspatial population dynamics, but also by differences in approaches to uncertainty and precaution. In federal fishery management on the U.S. West Coast, certain values of SPR (FLEP) are targeted as proxies for MSY based on simulations by Clark (1991). Uncertainty is incorporated in this decision process by considering different states of nature (often the value of CRT), and precaution is pursued by reducing the recommended catch when there is greater uncertainty. By contrast, in our analysis of a system in which MPAs are embedded within a conventional fishery, both CRT and FLEP values are taken to be uncertain states of nature affecting population persistence, and precaution involves designing networks with more habitat in MPAs, since catch outside of MPAs cannot be altered within the MPA design process. A means to effectively consolidate these two approaches to handling uncertainty and precaution for populations managed both conventionally and with MPAs is still needed (Field et al. 2006, Botsford et al. 2008).

By design, MPAs affect multiple species, and the best way to summarize the performance of an MPA for multiple species is unclear. The two alternatives we considered, an unweighted mean across all species and a mean weighted by commercial fishery value, produced similar recommendations. The results weighted by commercial value were dominated by the highly valuable red sea urchin fishery. Because sea urchins have highly dispersive larvae but limited mobility as adults, our model predicted that they would be well protected under most proposed MPA networks. This caused the commercial-value-weighted results to be somewhat rosier than the unweighted results. This is a potential drawback of this sort of weighting scheme: proposals will be penalized very lightly for failing to protect low-value species, undermining any non-fishery (i.e., biodiversity) goals of the MPA (Hastings and Botsford 2003). On the other hand, an unweighted mean across many species could dilute the costs (or benefits) of the MPA for high-value target species. In short, the list of species and their weightings must be chosen with care. In general, weighting species based on current commercial value may not capture their true economic value, but the commercial harvest values were the only reliable data available to us. Future efforts should attempt to incorporate values to recreational fisheries and nonconsumptive users as well (Klein et al. 2009). Additionally, it may be desirable to account for interactions among the target species (Micheli et al. 2004, Baskett et al. 2006) as the data required to do so become available.

Investigators using bioeconomic models have pointed out that profit, not yield, is the proper currency for determining and maximizing the efficacy of fishery management strategies (Clark 2005), including marine reserves (Sanchirico et al. 2006, White et al. 2008). We



agree with these authors that economic considerations will generally prevent harvest rates from reaching “scorched earth” levels, but we find it equally unlikely that they will meet optimized targets (Botsford et al. 1997). In any case, optimizing MPA configurations was not our goal; rather we sought to describe an approach for handling uncertainty, and the same decision analysis framework could use profit instead of yield as a response variable. Modeling profit could be especially informative if the description of fishing fleet behavior accounted for fishing effort and travel costs from fishing ports (Smith and Wilen 2003).

One additional caveat is necessary in interpreting the results of the infinite coastline model (Fig. 1). The two hypothetical species modeled there were assumed to have very long larval dispersal distances relative to the size of individual MPAs. We took this approach in part because the effects of MPAs on persistence of long-distance dispersers is much more sensitive to spatial configurations of MPAs and habitat, as well as fishing (Kaplan et al. 2009). As a result, no single MPA received enough settlement of locally produced larvae to sustain a self-persistent population (Botsford et al. 2001), and population persistence was dependent on a network effect (*sensu* Hastings and Botsford 2006) in which reproductive output across the entire MPA network sustained the population along the entire coast. The result that some minimum fraction of the coastline must be in MPAs in order to sustain a persistent population (Fig. 1a, b) depends on that assumption of long dispersal distances. For shorter-distance dispersers, population persistence is possible within a single MPA and recruitment increases monotonically with the fraction of the coastline in MPAs (Botsford et al. 2001, Kaplan et al. 2006). This type of situation was observed in the California example in the results for red abalone (Fig. 3a, c, e), which has very short-distance larval dispersal.

As MPAs grow in popularity, it becomes increasingly important to evaluate their effectiveness as both conservation and fishery management tools (CDFG 2008, Claudet et al. 2008, Lester et al. 2009). When policy makers and their scientific advisors set goals for MPA performance, it is crucial that they understand the influence of conventional management on population dynamics with the MPAs. Indeed, since it is generally impractical to propose different MPA boundaries for different species, successful management of species assemblages in MPA networks will have to proceed by tuning conventional fishery regulations outside of MPA boundaries on a species-by-species basis. Ideally, spatially explicit, tactical models of MPA performance such as ours could be integrated into existing ecosystem-based management tools, such as management strategy evaluation (Sainsbury et al. 2000, Smith et al. 2007), and also used in the adaptive management process after initial MPA implementation (Christensen et al. 1996). Careful use of decision-analytic frameworks such as the one presented here should assist in quantifying uncer-

tainties and codifying predictions about the future in order to choose appropriate MPA designs and set realistic performance goals for them.

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#### APPENDIX A

Summary of fishery stock information used to obtain values of the fraction of lifetime egg production (FLEP) and critical replacement threshold (CRT) (*Ecological Archives* A020-057-A1).

#### APPENDIX B

Life history parameters for California North Central Coast species (*Ecological Archives* A020-057-A2).

#### APPENDIX C

Proposed marine protected areas in the California North Central Coast region and description of one-dimensional representation of two-dimensional coastal habitat maps (*Ecological Archives* A020-057-A3).