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The utility and limitations of size and spacing guidelines for designing marine protected area (MPA) networks

Elizabeth A. Moffitt *, J. Wilson White, Louis W. Botsford

Department of Wildlife, Fish and Conservation Biology, University of California, Davis One Shields Ave., Davis, CA 95616, USA

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ABSTRACT

Marine protected areas (MPAs) implemented to conserve biodiversity must protect many species with a broad range of movement characteristics. To meet that goal, size and spacing guidelines have been used in MPA network design as a proxy for explicitly representing connectivity and species movement. However, there has been no assessment of the biological effects of these simple rules. We evaluated these guidelines by estimating population persistence with a spatially explicit population model over: (1) an idealized coastline and (2) an example from California, USA. Persistence of a species within an MPA network depends strongly on its movement characteristics; therefore we used the number of combinations of larval dispersal distances and adult home range diameters as an index representing the number of species that could be protected by a MPA network. The index of species protected usually increased steadily with increasing MPA size. By contrast, decreasing MPA spacing only produced large increases in the index when spacing became close enough to allow species persistence via network connectivity rather than self replenishment. Species persistence also depended on the exploitation rate outside MPAs. Size and spacing guidelines are a simple and useful way to begin the MPA network design process, but meeting these guidelines does not guarantee persistence for all populations one may wish to protect. The use of spatially explicit population dynamics models that evaluate population persistence directly provides a more comprehensive basis for comparing proposed MPA network designs.

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1. Introduction

Marine protected areas (MPAs) are locations where certain anthropogenic disturbances (primarily fishing) are prohibited with the goal of conserving biodiversity and/or improving fisheries management. The fundamental questions in MPA network design regard the size, placement, and number of MPAs required to protect desired species, with the fundamental metric of "protection" being population persistence. Effective MPA design is complicated by the movement of organisms across MPA boundaries. Marine organisms vary greatly in their movement ability, both in the planktonic larval stage (Kinlan and Gaines, 2003) and as adults (Lowe and Bray, 2006). Species with smaller spatial scales of larval and adult movement are typically better protected from fishing mortality within individual MPAs than widely-dispersing species (species that move far require larger MPAs) (Botsford et al., 2001; DeMartini, 1993; Kaplan et al., 2009; Moffitt et al., 2009; Polacheck, 1990), yet in order to conserve biodiversity, species with a broad range of movement characteristics must persist within the MPA network.

Modeling and empirical studies have shown that different spatial considerations allow persistence of species with specific larval and adult movement parameters. Persistence of populations in MPAs can be understood in terms of replacement: on average, individuals must reproduce enough to replace themselves within their lifetimes. Studies of marine populations with dispersing larvae have revealed two ways in which populations can have sufficient replacement to persist in a system of MPAs: (1) self-persistence and (2) network persistence (Botsford et al., 2001; Hastings and Botsford, 2006). In the self-persistent case, enough locally produced larvae return to the same MPA to maintain individual replacement, regardless of contributions from other locations. Replacement via network persistence occurs through multiple dispersal paths connecting MPAs over several generations. Species with short larval dispersal distances will generally be able to maintain self-persistent populations within MPAs, whereas species with long larval dispersal distances will typically exhibit network persistence (e.g., White et al., 2010a). In general, MPA network design affects population persistence through two key variables: (1) the size of individual MPAs, which affects the protection of mobile adult individuals from fishing mortality

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* Corresponding author. Present address: School of Aquatic and Fishery Sciences, University of Washington, 1122 NE Boat St., Box 355020, Seattle, WA 98195, USA. Tel.: +1 206 526 4694; fax: +1 206 526 6723.

E-mail addresses: emoffitt@uw.edu (E.A. Moffitt), whitejw@uncw.edu (J. Wilson White), lwbotsford@ucdavis.edu (L.W. Botsford).

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(DeMartini, 1993; Moffitt et al., 2009; Polacheck, 1990) and whether an MPA receives a sufficient fraction of locally produced larvae to be self-persistent (Botsford et al., 2009); and (2) the total fraction of a coastal region contained in MPAs, which determines network persistence (Botsford et al., 2001; Hastings and Botsford, 2006).

Strategies for designing MPA networks require a means for deciding which areas to set aside in MPAs in order to meet the goal of persistence of multiple species. One approach relies on optimization algorithms to choose the combination of MPAs that best meets habitat representation goals. This approach has been applied to MPA network design problems worldwide (e.g., Fernandes et al., 2005; Airame et al., 2003; Sala et al., 2002). A critical assumption of this approach is that the resulting spatial configuration of habitat will support persistent populations of a range of species, an assumption that may not hold true.

A second approach to MPA network design simulates population dynamics in order to determine whether a proposed MPA network would be expected to support persistent populations of species with certain movement characteristics. This approach is based on modeling results that show the dependence of population persistence within an MPA network on species' larval dispersal and adult home range sizes relative to MPA size and spacing (Botsford et al., 2001; Kaplan et al., 2006, 2009; Moffitt et al., 2009; White et al., 2010b). The combination of species predicted to be persistent can then be used as a criterion for comparing alternative MPA network proposals. Insofar as the goals of an MPA network require the presence of persistent populations, a direct evaluation of persistence criteria using population models may be superior to a proxy based on habitat representation (as is used in the optimization approach), since the persistence calculation accounts for both the spatial distribution of habitat and the movement of individual organisms.

A shortcut around direct simulations of population persistence for MPA network design is the use of "size and spacing" guidelines, which set a minimum size for each MPA and a maximum distance between MPAs in an effort to ensure the persistence of a suite of species in an MPA network. For example, the minimum size of the MPA could be set to be greater than the adult home range for target species and maximum spacing between MPAs could be set to allow some larval exchange between MPAs (Halpern et al., 2006; Palumbi, 2004; Shanks et al., 2003). Size and spacing guidelines are currently being used in the MPA network design process underway along the coast of California, USA (CDFG, 2009). They are used not only to inform the initial design of proposed MPA networks, but also in the evaluation of candidate network proposals. It is presumed that size and spacing guidelines account for the effects of larval connectivity and adult movement on MPA performance, and candidate MPA network designs are judged by how well they meet the guidelines. However, there has been no evaluation of the effectiveness of these simple rules in terms of the range of species that would have persistent populations if the guidelines were followed. At present, California is the only jurisdiction in which size and spacing guidelines have been used in MPA network design. However, MPA design theory is rapidly developing, and California's currently implemented MPA network is among the largest in the world. Marine managers worldwide are likely to look to California for guidance in designing MPA networks; the state of Oregon has already sought advice from scientists involved in California's process (Heppell et al., 2008). MPA network design requires deciding which areas of a region to set aside, and decision-makers are likely to find simple size and spacing guidelines to be an attractive alternative to estimating which species will likely persist in a proposed spatial configuration of MPAs. Thus a formal evaluation of the efficacy and usefulness of such guidelines is timely.

Here we evaluate the use of size and spacing guidelines in MPA network design by using spatially explicit population models to evaluate whether MPAs with different size and spacing configurations actually support persistent populations. We perform this analysis using models of an idealized coastline and illustrate our findings with an example from California.

2. Methods

2.1. Policy background

In 1999, the California legislature passed the Marine Life Protection Act (MLPA), which called for a comprehensive network of MPAs to be implemented in state-managed waters (offshore to 5.56 km; CDFG, 2009). The California Department of Fish and Game divided the state coastline into five study regions, with MPA networks designed and implemented on a region-by-region basis. Within each region, local stakeholder groups propose competing MPA network proposals, a Science Advisory Team provides guidance and comparative evaluation of stakeholder proposals, a Blue Ribbon Task Force provides policy guidance, and the Fish and Game Commission chooses a final MPA array for implementation.

The Science Advisory Team for the first study region, the Central Coast, developed guidelines for MPA size and spacing, which specified that MPAs should extend from the intertidal zone to the offshore boundary of state-managed waters (leading to MPAs of approximately 5.56 km in cross-shelf width) and be at least 5 km (minimum) or 10–20 km (preferred) in alongshore length and spaced 50–100 km apart. These guidelines were based on available knowledge of the distribution of adult home range sizes and larval dispersal distances, respectively, for local nearshore species (CDFG, 2009). In that study region and all subsequent study regions, stakeholder-designed MPA networks have been evaluated based on how well they meet these size and spacing guidelines (among other criteria). In later study regions, evaluations have also been based on the results of spatially explicit population models such as those described below, but these models have not supplanted the use of size and spacing guidelines.

2.2. Population model

To evaluate the efficacy of size and spacing guidelines, we used a spatially explicit population model to predict whether populations of hypothetical species with a particular combination of adult home range size and larval dispersal distance would persist in a hypothetical MPA network with a given size and spacing configuration. The model was age-structured with density-dependent recruitment, extended along a one-dimensional coastline, and generally follows the models used by Kaplan et al. (2009) and Moffitt et al. (2009). Replacement was represented in terms of lifetime egg production (LEP), and is given here as the fraction of unfished, natural LEP (FLEP).

The replacement criterion for population persistence, that individuals in a population must replace themselves within their lifetimes, is well known for single, non-spatial populations. Because it is common for marine species to produce many eggs that disperse via ocean currents, it is usually difficult to evaluate this criterion directly. Instead, fisheries biologists represent reproductive output in terms of how many eggs an average individual must produce during its lifetime to ensure that at least one survives the larval and juvenile stages (Goodyear, 1993; O'Farrell and Botsford, 2005; Sissenwine and Shepherd, 1987). The number of new recruits into a population that is produced from a given number of eggs or spawning adults is described by a stock-recruitment function. In a single, non-spatial population the minimum value of lifetime egg production (LEP) required for persistence is related to the form of the stock-recruitment relationship:

$$\mathrm{LEP} > \frac{1}{R'(0)} \tag{1}$$

where $R'(0)$ is the slope of the stock-recruitment curve at the origin (Goodyear, 1993; Sissenwine and Shepherd, 1987). We refer to this level of LEP at the origin as the critical replacement threshold (CRT). If LEP is reduced by fishing to be less than $1/R'(0)$, the equilibrium population size will go to zero and the population will collapse. To apply this relationship over many species, it is typically written nondimensionally in terms of the fraction of unfished LEP (FLEP), which spans 0 (scorched earth harvesting) to 1 (unfished). The CRT is then also expressed as a fraction, i.e., the value of FLEP below which population collapse occurs. It is necessary to harvest the population to low levels in order to determine the slope of the stock-recruitment function at the origin. Because this is not a desired outcome of proper management, the CRT is highly uncertain for most species. For those populations for which fishery biologists have had the data required to measure FLEP, they have found that values in the range of 25–60% avoid collapse (Clark, 2002; Dorn, 2002; Mace and Sissenwine, 1993; Myers et al., 1999; Ralston, 2002). In conventional, single population management, FLEP is assumed to be constant over large geographical areas, and the population is considered to be persistent if FLEP > CRT.

To use this criterion in the spatial context of MPAs, one must consider spatial heterogeneity in FLEP, which will be 1 inside no-take MPAs and <1 in fished areas. We used the dispersal-per-recruit (DPR) model (Kaplan et al., 2006, 2009; Moffitt et al., 2009) to determine which combinations of larval dispersal and adult movement would lead to a persistent population for a given MPA network. Dispersal-per-recruit is a spatial model that reduces the question of population persistence to calculations involving the spatial distribution of FLEP, critical replacement threshold (CRT), mean larval dispersal distance, and adult home range diameter. It accounts for all the pathways by which larvae can be dispersed to and return from each location in space. We used the iterative variant of DPR (Kaplan et al., 2006), which calculates the spatial distribution of recruitment (R_i) at equilibrium at each model location (i):

$$S_i = \sum_j D_{ji}\mathrm{FLEP}_j R_j \tag{2a}$$

$$R_i = f(S_i) \tag{2b}$$

A population is persistent in the model if equilibrium recruitment (R_i) is greater than the CRT at any point (i) along the coastline. The larval settlement (S_i) to location i along the coast was expressed as the sum of larval production (R_j) at all other location j times the probability of dispersal (D_{ji}) from those points to i. The probability of larval dispersal between points (D_{ji}) was modeled here by a Gaussian dispersal kernel (Siegel et al., 2003) with mean of zero (i.e., no advection). The standard deviation of the kernel defined the mean dispersal distance in one direction. If location i lacked suitable habitat, larvae could not disperse to that location, and dispersal from there was not possible, i.e., $D_{ji} = 0$ for all j. The relationship ($f(S)$) between settlers (S) and recruits (R), which incorporates post-dispersal density-dependence, was of a hockey-stick form, which increases linearly with settler density until a maximum value is reached and then is constant (Barrowman and Myers, 2000). The advantage of the hockey-stick function is that it is a simplification of the Beverton-Holt settler-recruit function and is defined solely by the slope at the origin and the maximum recruitment level. We chose the slope of the settler-recruit function to correspond to a critical replacement threshold (CRT) of 35% of natural unfished lifetime egg production (LEP), a CRT level that has been used for several fished species (Clark, 2002). In general, model results are affected by the value of CRT relative to FLEP, not the value of CRT per se; see Botsford et al. (2001) and White et al. (2010a) for examples with different combinations of FLEP and CRT. In the analyses presented here, a population is overfished and will not persist without MPAs when FLEP_i was below 35% at all locations i. Fecundity increased with mass, as is the case for many species, and length was modeled as a von Bertalanffy function (additional model details given in Moffitt et al., 2009).

The vulnerability (υ) to fishing mortality of individuals whose home range is centered at i is defined as the fraction of the home range that overlaps the fished area:

$$\upsilon_i = \frac{1}{H}\sum_{x=-H/2}^{x=+H/2} c_{i+x} \tag{3}$$

where H is the diameter of the home range, and c_{i+x} is defined as 0 for reserves and 1 for fished areas (Moffitt et al., 2009). Vulnerability to fishing mortality (υ_i) is incorporated into the calculation of FLEP by multiplying υ_i by the fishing mortality rate (F) in the survival term. As in Moffitt et al. (2009), we assumed that each individual's use of space within its home range followed a uniform distribution.

When habitat is continuous, population collapse occurs when FLEP is less than the CRT at all locations. When habitat is heterogeneous, a fraction of the larvae disperse to non-habitat locations where they cannot settle, and therefore do not grow into reproducing adults. This would cause population collapse to occur at FLEP levels greater than the CRT if $R'(0) = 1/\mathrm{CRT}$. In order to correct for this, we adjusted the slope of the settler-recruitment function at the origin as follows:

$$R'_a(0) = \frac{1}{\mathrm{CRT} \times l_D} \tag{4}$$

where l_D is the dominant eigenvalue of the larval dispersal matrix D_{ji}. This correction ensures that the persistence threshold was $\mathrm{FLEP}_i = \mathrm{CRT}$ for any heterogeneous distribution of habitat, and did not depend on dispersal distance (White, 2010a).

Representing fishing effects in terms of FLEP and CRT with the dispersal-per-recruit approach allows us to represent the dynamics of any generic species with a particular level of fishing and movement characteristics. However, actual life history parameters must be specified in order to make the calculations relating fishing mortality rate (F) to FLEP, so we used the relatively well-known life history parameters for black rockfish (*Sebastes melanops*) (Table 1), but the general nature of results does not depend on these (see Appendix A). For simplicity we assumed that all MPAs were no-take and protected all species from fishing mortality. We did not reallocate fishing effort from MPAs to fished areas because we are modeling equilibrium results after MPA establishment, and not comparing results before and after implementation.

2.3. Larval dispersal distances and adult home range sizes

Ideally we would want to model all species we wish to persist in a network of MPAs, but even in well-studied regions such as nearshore California, the necessary life history and movement parameters are not known for more than a handful of species (e.g., White et al., 2010b). Nonetheless, in spatial management, the defining characteristics of species are those associated with movement, so we used the fraction of combinations of larval dispersal distances and adult home range diameters that were persistent in model calculations as an index for number of species in a region that would be persistent within an MPA network (note that all other life history parameters relevant to persistence are subsumed within

Table 1
Sebastes melanops (black rockfish) life history parameters used to generate FLEP in analyses.

Parameter	Value	Definition	Source
L_∞	44.2	Asymptotic von Bertalanffy length (cm)	Bobko and Berkeley (2004)
k	0.33	von Bertalanffy growth parameter	Bobko and Berkeley (2004)
t_0	0.75	Age at which individual would be length 0	Bobko and Berkeley (2004)
a_{mat}	7	Age at 50% maturity	Bobko and Berkeley (2004)
Max age	50	Maximum age	Love et al. (2002)
d	1.677×10^{-5}	Coefficient in weight at length (kg)	Sampson (2007)
b	3	Exponent in weight at length	Sampson (2007)
M	0.14	Natural mortality rate	Sampson (2007)
t_c	7	Age at first capture in fishery	We chose this to correspond with a_{mat}
$Eggs = (f + g * weight) * weight$			
f	289,406	Parameter in weight–fecundity relationship	Sampson (2007)
g	103,076	Parameter in weight–fecundity relationship	Sampson (2007)

FLEP). This species index was defined as the fraction of *movement combinations* (the term we will use henceforth) in the set of home range and mean larval dispersal distances that are persistent in the coastline. The value of this fraction depends in the obvious way on the values of larval dispersal distances and home range sizes considered. The mean larval dispersal distances we considered in the analyses spanned distances from 0 to 100 km, values which are consistent with empirical estimates for species in this region (Kinlan and Gaines, 2003; Miller and Shanks, 2004; Shanks et al., 2003) (Fig. 1). We considered adult movement that spanned sedentary (0 km) to home ranges up to 40 km in diameter, a reasonable breadth based on measured home ranges for nearshore California temperate rocky reef fishes (Freiwald, 2009). Fig. 1 shows estimates of mean larval dispersal distances and home range diameters for black surfperch, lingcod, black rockfish, cabezon, and California scorpionfish. Lingcod, cabezon, and California scorpionfish lack estimates of mean larval dispersal distance. For these species we used the pelagic larval duration to estimate mean larval dispersal distance (Shanks et al., 2003).

At present, information is available for too few species to determine the true distribution of movement combinations within the two-dimensional parameter space of larval dispersal and adult movement distances. Therefore, we made the simplifying and parsimonious assumption that species are uniformly distributed across those two dimensions. While the available data for California species do not contradict this assumption directly (Fig. 1), we note that determining the true distribution of species within the movement parameter space from existing measurements is limited by the number of studies and is also potentially biased because measurements of larval dispersal and adult home range are likely more common for commercially important species and for species with limited movement.

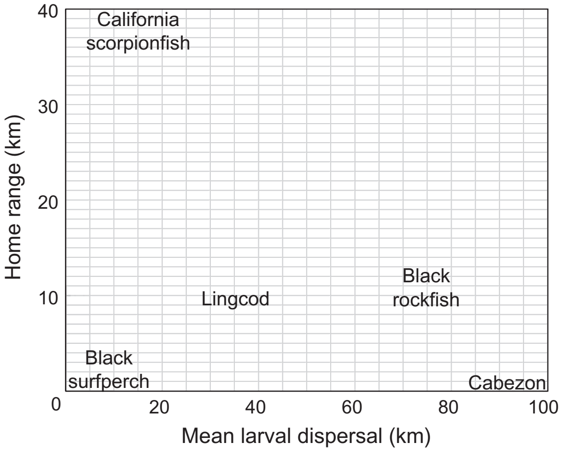

Fig. 1. The set of mean larval dispersal distances and home range lengths used in the model as an index of species. Reasonable estimates of mean larval dispersal distances and home range diameters for black surfperch (*Embiotoca jacksoni*) (Hixon, 1981; Love, 1996), lingcod (*Ophiodon elongatus*) (Cass et al., 1990; Jagielo, 1990; Lea et al., 1999; Marko et al., 2007; Martell et al., 2000; Starr and Green, 2007; Starr et al., 2004), black rockfish (*Sebastes melanops*) (Culver, 1987; Mathews and Barker, 1984; Miller and Shanks, 2004; Starr and Green, 2007; White et al., 2010b), cabezon (*Scorpaenichthys marmoratus*) (Cope and Punt, 2005; C. Merelis, R. Nakamura, and D. Wendt, unpublished manuscript), and California scorpionfish (*Scorpaena guttata*) (Carr and Reed, 1993; Hartmann, 1987; Love, 1996; Love et al., 1987) are shown.

2.4. General patterns of population persistence

We first evaluated the efficacy of size and spacing guidelines by calculating the fraction of movement combinations that were persistent in MPA networks with a variety of size and spacing configurations. We modeled populations on a linear coastline of infinite length. An infinite coastline was used in order to avoid the idiosyncratic effects of larvae and adults being lost at the edges of the model domain, but persistence was calculated on one repeating section only. We assumed constant habitat along the coast so that we could evaluate the effects of changing MPA size and spacing without the confounding effects of patchily distributed habitat specific to a particular coastline. This approach corresponds to the original model formulations that motivated most size and spacing recommendations (Botsford et al., 2001, Gaines et al. 2003). We examined MPA configurations with size ranging from 0 (no MPAs) to 100 km, and spacing ranging from 0 to 100 km. Note that the model coastline was one-dimensional, so MPA "size" refers only to the alongshore length. For each combination of size and spacing, we calculated how many movement combinations (i.e., species) would persist in that network. Because persistence results depend strongly on the level of exploitation (Botsford et al., 2001; Holland and Brazee, 1996; White et al., 2010b), we evaluated four levels of FLEP outside MPAs (FLEP > 0.35 and FLEP = 0.30, 0.20 and 0.10). For the first value of FLEP the population is not being overfished. The last three FLEP values correspond to overfishing, with the level of exploitation increasing as FLEP decreases.

2.5. Case study: Central California Coast

To examine the utility of size and spacing guidelines in a real-world example, we also applied our model evaluations to California's Central Coast. Within the MLPA process, MPAs were typically designed such that each no-take State Marine Reserve abutted a limited-take State Marine Conservation Area. The pair forms an MPA 'cluster', which size and spacing analysis treated as a single unit. With MPAs 2.3–12.5 km in alongshore length, not all MPA clusters in the final network approved by the California

Fish and Game Commission (the “Commission Package”) met the preferred size guidelines. In order to determine whether the performance of the Commission package would improve if all of its MPA clusters met the preferred size guidelines (10–20 km in length), we created alternative MPA networks in which clusters were adjusted to meet the preferred size guidelines. We created alternative networks following two general procedures. In the add area (“A”) approach, undersized clusters in the Commission package were lengthened so that all MPAs had minimum size 10 km (“10A”) or 20 km (“20A”). The former met the lower end of the preferred size guidelines, while the latter met the upper end. In the A approach, increasing MPA size also necessarily decreased MPA spacing. In order to examine the effects of increasing MPA size while holding average spacing relatively constant, we also implemented a conserve area (“C”) approach, in which some undersized clusters in the Commission package were lengthened, some were removed, and some oversized clusters were shortened such that total MPA area remained constant but all MPAs had minimum size 10 km (“10C”) or 20 km (“20C”). There are a large number of different possible ways that the Commission package could be altered to meet those four target criteria (10A, 20A, 10C, and 20C), so we used a random algorithm to simulate 100 alternative MPA configurations for each of the four criteria. The algorithm proceeded by adding MPA area in 2.3 km increments (the minimum model grid size) to a randomly selected edge of a randomly selected MPA, then repeating that process until all MPAs in the array met the minimum size criterion. For the C procedure, each addition of MPA area was paired with the deletion of a single 2.3 km increment from a randomly selected MPA that exceeded the size guidelines.

Digital maps of the Commission package MPA boundaries and nearshore rocky habitat were obtained from the California Department of Fish and Game. Habitat data were provided in two depth categories, 0–30 m and 30–100 m. For simplicity, we only modeled species occupying the 0–30 m zone. We converted rocky bottom habitat maps and the Commission package into a one-dimensional domain using the same procedure as Kaplan et al. (2009). Habitat north but not south of the study region was included in the model domain, as Point Conception (to the south) is considered a natural oceanographic break. This produced a linear domain of 251 model cells, each of length 2.3 km. The alternative MPA networks were created by adjusting the Commission package in this linear domain, not on the original two-dimensional map. We then ran the DPR population model using this linear model domain. Note that unlike the infinite coastline case, it was now possible for larvae to disperse across the edge of the domain and be lost, and we assumed that larvae settling in model cells lacking appropriate hard-bottom had FLEP = 0 (i.e., they died without reproducing). Note that hereafter all references to MPA “size” indicate the alongshore dimension in this model domain (in practice all MPA clusters had the same cross-shore width because they all extended from the beach to the boundary of California territorial waters).

3. Results

3.1. Generalized coastline

Examples of the implementation of the MLPA guidelines for overfished populations (in this case FLEP = 0.20) illustrate the complexity of possible responses. A network of 5 km MPAs spaced 100 km apart conforms to the minimum size and spacing guidelines, but led to persistence for only 2.0% of the index of the number of species protected (the fraction of movement combinations persistent); those species with limited adult and larval movement (⩽11 km home range, ⩽10 km larval dispersal distance) (Fig. 2a). For this scenario, only low-movement species such as black surfperch would persist. Decreasing the spacing from 100 km to 50 km did not increase the fraction of movement combinations that were persistent (Fig. 2a). A network of 10 km MPAs spaced 100 km apart met the size guidelines and led to population persistence for 6.1% of the considered movement combinations (Fig. 2b). Ten km MPAs supported persistent populations for slightly more movement combinations (6.4%) when spacing was reduced to 50 km.

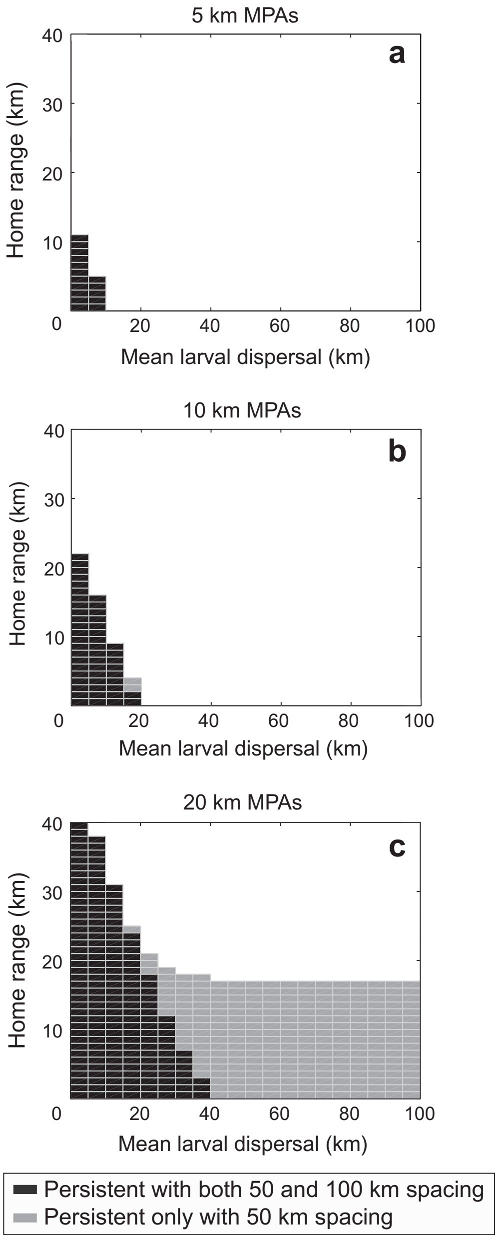

Fig. 2. The set of species (in terms of mean larval dispersal distance and adult home range length) with persistent populations in a network of MPAs, each MPA measuring 5 km (a), 10 km (b), and 20 km (c) in length and spaced either 50 or 100 km apart in a generalized infinite coastline of continuous habitat. Fraction of lifetime egg production (FLEP) outside MPAs is 0.20.

A network of MPAs 20 km in length met the upper bound of the preferred size guidelines and led to population persistence for a larger set of movement combinations (Fig. 2c). With MPAs this large, decreasing spacing produced a more substantial effect. MPAs of 20 km length protected a much larger range of movement combinations when spaced 50 km apart (51.8%) than when spaced 100 km apart (21.6%). This increase occurred because persistence of populations with large mean larval dispersal was maintained through a network effect, rather than self-persistence (Botsford et al., 2001; Hastings and Botsford, 2006; Kaplan et al., 2009). In this scenario, species with movement combinations corresponding to black surfperch, lingcod, black rockfish, and cabezon persisted in the model.

It is important to note that by varying both size and spacing, we were indirectly varying the total fraction of the coastline in MPAs. We examined the relative effects of size and spacing by considering networks with the same fraction of the coastline in MPAs but different size and spacing configurations. In such cases, the network with larger MPAs always led to persistent populations for a broader set of movement combinations. For example, a network of 5 km MPAs spaced 50 km apart and a network of 10 km MPAs spaced 100 km apart both cover 9.1% of the coastline in MPAs, but the latter led to population persistence for a broader set of movement combinations (6.1% vs. 2.0%) (Fig. 2a and b).

We next analyzed the fraction of movement combinations that were persistent for many more combinations of MPA size and spacing at several different levels of exploitation rate (FLEP) outside MPAs in order to explore the marginal benefit of incremental increases in size or decreases in spacing (Figs. 3 and 4). The results of this analysis were summarized as the fraction of persistent movement combinations within a coastline covered by MPAs of a particular size and spacing (i.e., the graphical results for each size and spacing combination in Fig. 2 were summarized as single values). We first considered the effects of MPA size, with spacing held constant at 100 km or 50 km (Fig. 3). The relationship between MPA size and the fraction of persistent movement combinations was generally sigmoidal: the marginal benefit of making MPAs larger initially increased with MPA size, but gradually leveled off as the fraction of persistent movement combinations approached 100%. The results did not change greatly between 50 and 100 km spacing, but did depend on the FLEP level outside MPAs. As populations became less overfished (FLEP increased), more movement combinations were persistent. When FLEP was greater than the CRT of 0.35, all movement combinations were persistent with or without MPAs (Fig. 3).

We also examined the effects of decreasing spacing on the fraction of movement combinations that were persistent for 5, 10, and 20 km long MPAs (Fig. 4). Consistent with previous results, the fraction of persistent movement combinations depended greatly on exploitation rate (FLEP) outside MPAs. Also, decreasing spacing from large values did not lead to persistence for a greater fraction

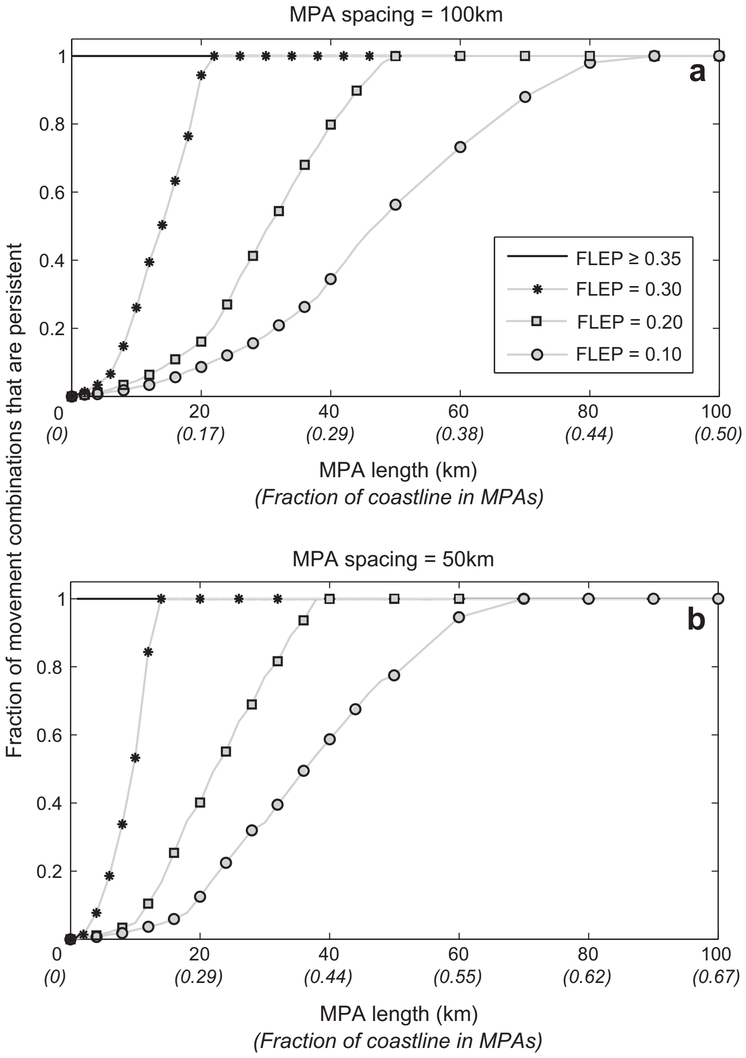

Fig. 3. The fraction of larval dispersal and home range combinations persistent (e.g., the shaded area of persistent populations in Fig. 2) in a network of MPAs of a given length, spaced 100 km (a) and 50 km (b) in an infinite coastline with continuous habitat. Mean larval dispersal distances and home range lengths in the set span 0–100 km and 0–40 km, respectively. Results for FLEP values of 0.10, 0.20, 0.30, and ⩾0.35 are plotted. The fraction of the coastline in MPAs is also shown. Extraneous data points were removed from the plots to improve clarity.

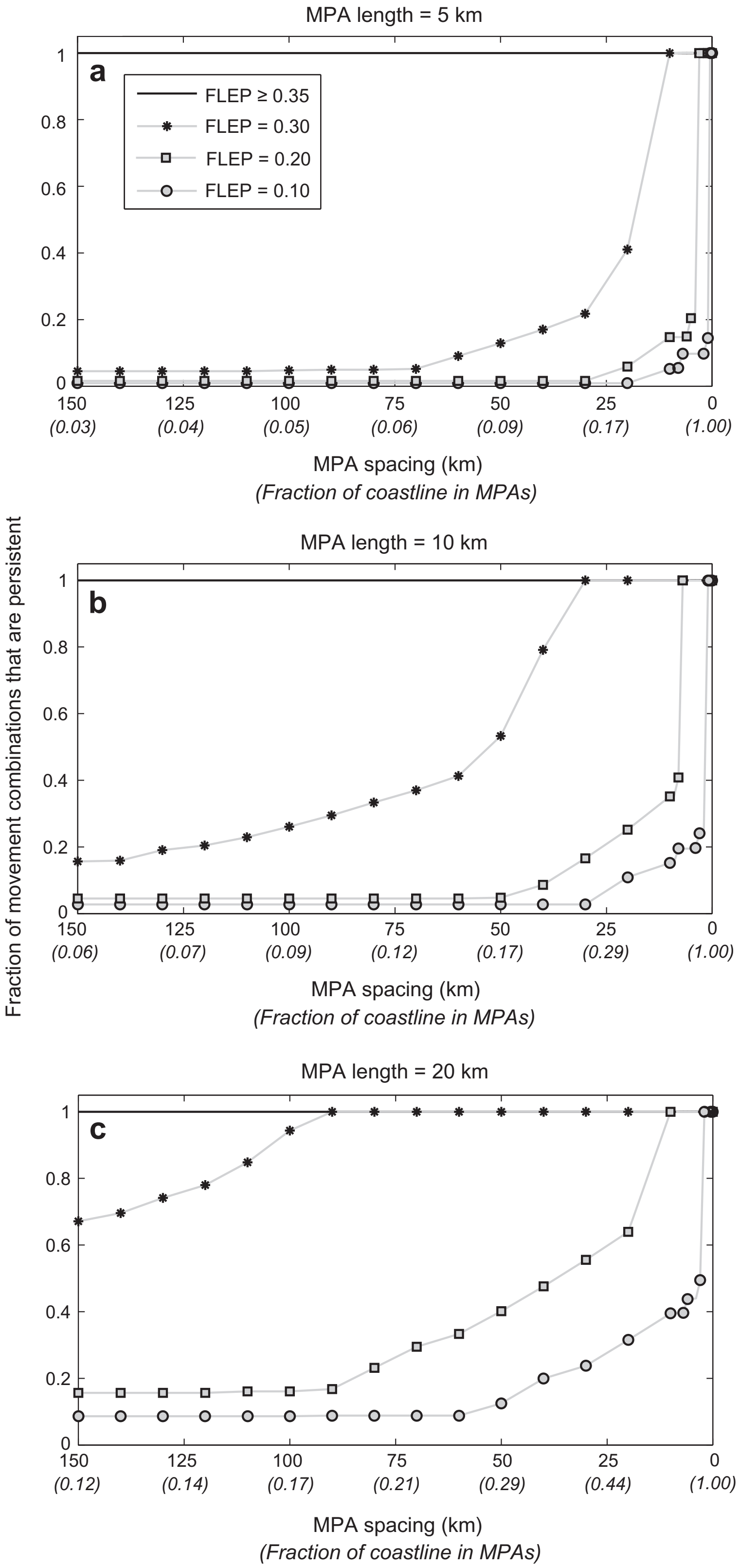

Fig. 4. The fraction of larval dispersal and home range combinations persistent in a network of 5 km (a), 10 km (b), and 20 km (c) MPAs for an array of MPA spacing in an infinite coastline with continuous habitat. Mean larval dispersal distances and home range lengths in the set span 0–100 km and 0–40 km, respectively. Results for FLEP values of 0.10, 0.20, 0.30, and ⩾0.35 are plotted. The fraction of the coastline in MPAs is also shown. Extraneous data points were removed from the plots to improve clarity.

of movement combinations until a certain threshold spacing was reached, at which point increases in the fraction of persistent movement combinations started to occur rapidly. This apparently occurred when the total MPA area became great enough to allow the system to shift from supporting a few self-persistent species to supporting network persistence for many species. The spacing at which this network persistence threshold occurred increased noticeably when the MPA themselves were larger in size (compare Fig. 4a–c). Notably, the converse was not true: spacing had little effect on the relationship between MPA size and population persistence (Fig. 3).

3.2. Case study: Central California Coast

We created four alternative MPA networks (10A, 10C, 20A, and 20C) in which MPA clusters in the Commission approved network were adjusted to meet the preferred size guidelines (Fig. 5). Because our modifications of MPA size had the effect of changing spacing as well, we plotted the persistence results for mean MPA size and mean inter-MPA spacing (Fig. 6).

Increasing MPA size often led to increases (relative to the Commission package) in the fraction of persistent movement combinations, even when the increase in size came at the expense of increased spacing between MPAs (Cases 10C and 20C; Fig. 6). An exception was for package 10C alternative configurations, which led to persistence for a similar fraction of movement combinations as the Commission package (Fig. 6a and b). Not surprisingly, package alternatives 20A, with the largest MPAs and spacing unchanged (on average) from the Commission package, led to persistence for the largest fraction of movement combinations (note that average spacing did not decrease substantially in the 20A scenario because closely-spaced MPAs were often merged into a single large MPA). Package 20C alternatives generally outperformed all packages except 20A even though they had much greater inter-MPA spacing than 10C, 10A, or the Commission packages. For populations that were less severely overexploited (FLEP = 0.20), a greater fraction of movement combinations were persistent (Fig. 6b). For the FLEP = 0.30 scenario, the Commission package (and all other alternatives) led to persistent populations for all movement combinations considered (Fig. 6c).

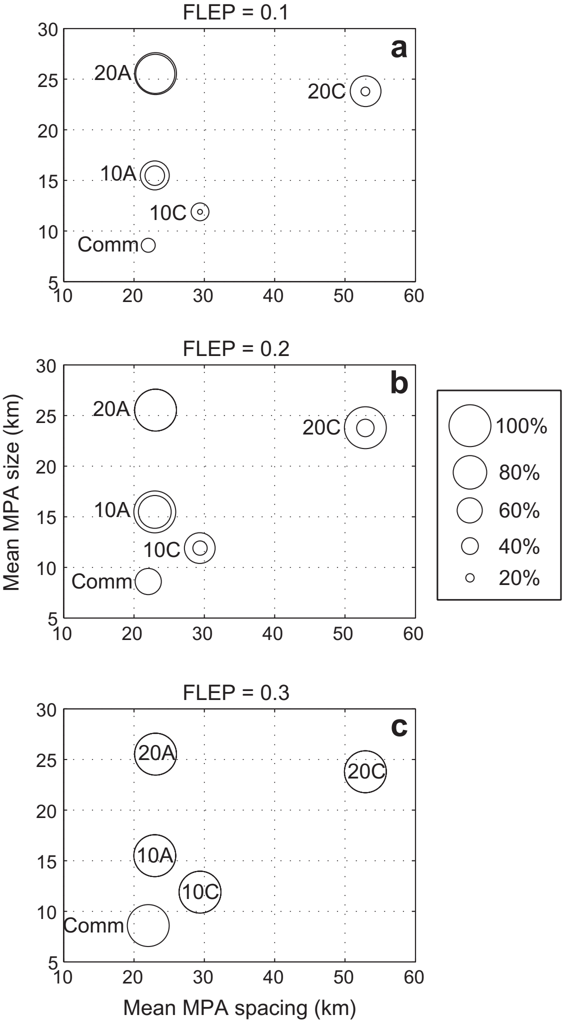

Fig. 6. The fraction of larval dispersal and home range combinations persistent for the California Central Coast Commission (Comm) and modified (10C, 10A, 20C, and 20A) MPA networks. The fraction of larval dispersal and home range combinations with persistent populations in an array are indicated by the size of the circle. For each modified array, the two circles are the 2.5% and 97% quantiles of the fraction of persistent movement combinations. Marker placement indicates the mean size and spacing for MPAs in each array. Mean larval dispersal distances and home range lengths in the set span 0–100 km and 0–40 km, respectively. Results are shown for FLEP values of (a) 0.10, (b) 0.20, and (c) 0.30 are shown.

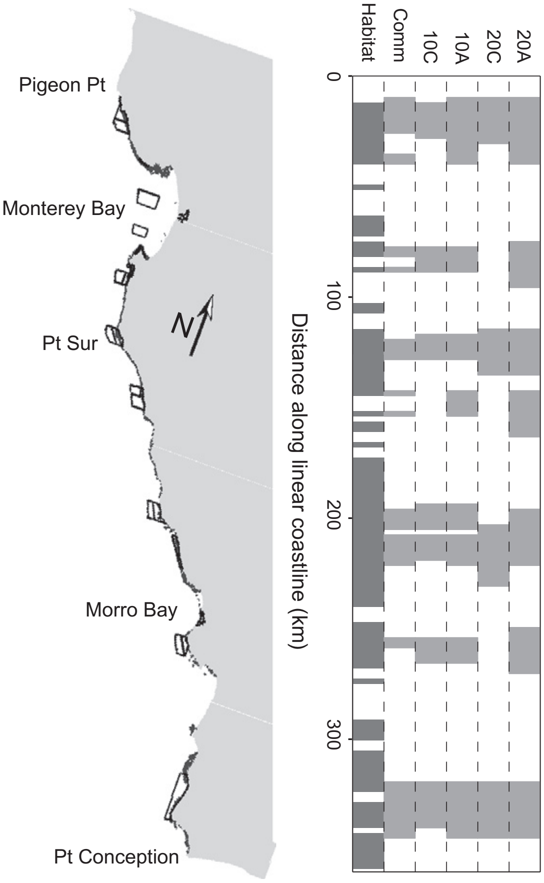

Fig. 5. (a) The Central Coast region of California from Pigeon Point to Point Conception with the Commission package of MPAs outlined. Rocky bottom habitat in depth 0–30 m is shown in dark gray. (b) The one-dimensional representations of the two-dimensional maps of rocky ('Habitat') and several MPA network configurations. MPAs in the Commission package (Comm) were modified to better meet the preferred size guidelines of 10 or 20 km by two methods; adding MPA coverage (10A and 20A) and conserving MPA coverage (10C and 20C). One hundred random configurations were generated for each of the four approaches; one representative example of each is shown.

In general, the fraction of persistent movement combinations depended on FLEP level and increased as MPA size increased, but did not depend greatly on MPA spacing. While 10C and 20C contained the same fraction of coastline in MPAs as the Commission package (and had greater average spacing), the fraction of persistent movement combinations was higher in 20C due to the larger MPA size.

4. Discussion and conclusions

The fundamental questions in MPA network design regard the size, placement, and number of MPAs required to protect desired species, with the fundamental metric of "protection" being population persistence. Whether an MPA network will support persistent populations can be evaluated directly using age- and spatially-structured models. Here, we addressed the question of whether MPA size and spacing guidelines are an effective proxy for the results of population dynamics models and how model predictions of persistence vary with changes in MPA size and spacing.

Our analyses showed that increasing size and/or decreasing spacing was especially critical for species with extensive movement in either the larval or adult stages, but that increasing MPA size generally led to greater increases in the fraction of movement combinations that were persistent than did decreasing MPA spacing. Decreasing spacing between MPAs did not lead to persistence for a greater fraction of movement combinations except in limited cases; often decreasing spacing did not change the results at all (Fig. 4). These modeling results are supported by the empirical results of a recent meta-analysis of the performance of European MPAs, in which larger MPAs were found to have larger increases in densities of commercially targeted fish than smaller MPAs, while efficacy was not affected by the distance to the nearest neighboring MPA (Claudet et al., 2008).

These results were also consistent with existing MPA design theory. It appears that increasing MPA size had a greater effect on persistence of movement combinations than did decreasing spacing because MPA size not only determines the protection of adults from fishing mortality (Moffitt et al., 2009), but also determines the mean larval dispersal distances protected in the MPA due to self-persistence (Botsford et al., 2001). In contrast, MPA spacing only affects persistence via its relationship to the fraction of coastline contained in MPAs, which determines whether species will exhibit network persistence. Once larval dispersal distances are long enough (or MPA spacing small enough) for network persistence to occur, there is essentially no relationship between dispersal distance and the fraction of the coastline needed for persistence; rather, the fraction is entirely determined by the level of exploitation (FLEP relative to the CRT) and home range size (Botsford et al., 2001; Moffitt et al., 2009).

The movement of species is a key uncertainty in spatial management. The fraction of movement combinations that are persistent appears to be a useful index of species richness for MPA network design, given the current lack of knowledge of many species' mean larval dispersal distances and home ranges. Despite efforts to measure larval dispersal distances, this parameter is not known for any species with great certainty (Botsford et al., 2009). Fortunately, if dispersal distances are sufficiently large, the minimum MPA area needed for network persistence is not sensitive to larval dispersal distance, and persistence calculations depend primarily on home range size and the fishing rate. Home range sizes can be measured more directly than mean larval dispersal distances, and are relatively well known for the limited number of species for which they have been measured. In analyses of persistence for several California species (White et al., 2010b), there is no indication that species diverge strongly from the uniform distribution assumed in our analysis. Even lacking the data required to better characterize the distribution of species within the movement parameter space, our method of using the fraction of movement combinations that are persistent as an index of species richness is a step beyond simple size and spacing guidelines. Of course in a system where the distribution is known to be non-uniform, the best-fit distribution of movement combinations should be used. Although the central results of our analyses do not depend on the specific distribution of species in the movement parameter space, the precision of the index will be improved for a particular area by the use of a best-fit distribution, if feasible. We note the obvious caution that the quantitative values of this index depend on the maximum values of mean larval dispersal distances and home ranges deemed most appropriate for the region.

Evaluating MPAs by gauging how well they meet size and spacing guidelines misses effects that can be seen with a more comprehensive evaluation using population modeling as illustrated in this paper. In particular, size and spacing assume that both benthic habitat and larval dispersal patterns are spatially homogenous. If larval dispersal distances are shorter for individuals spawning in certain locations, self-persistence is more likely for MPAs placed in those locations (White et al., 2010a), a nuance not captured by size and spacing guidelines. Additionally, size and spacing guidelines cannot represent the strong relationship between MPA performance and the exploitation level outside MPAs which may vary among species (White et al., 2010b). For example, for severely overfished populations (FLEP = 0.10), increasing MPA size from 5 km to 20 km did not lead to a large improvement in persistent populations, while for less severely overfished populations (FLEP = 0.30) it did (Fig. 3). This type of result is inconsistent with the premise of size and spacing guidelines, under which any increase in MPA size or decrease in spacing is considered a worthwhile improvement.

The determination of appropriate MPA networks depends on the set of species (with particular movement parameters) we wish to persist in MPAs under future exploitation scenarios. As we increase size and/or decrease spacing of MPAs, species with larger movement can become persistent in an MPA network, and more species will be expected to persist in the MPA network. But including more coastline in MPAs often involves social and economic costs (Klein et al., 2008). The decision of what the size and spacing should be lies at the cusp of science and policy. The number and types of species chosen to persist in an MPA network is a policy decision. But once that decision has been made, scientists can provide guidance and advice on how to do so.

Size and spacing guidelines are a simple and useful way to begin the MPA network design process, but meeting the guidelines does not guarantee persistence for all species managers may wish to protect, and the guidelines should be used only with full knowledge of their assumptions and limitations, as shown here. A better method in the comparison of proposed MPA networks is to use spatially explicit population dynamics models that evaluate population persistence directly (Kaplan et al., 2009; Walters et al., 2007; White et al., 2010b). Nonetheless, for cases in which size and spacing guidelines are the only feasible method for MPA network evaluation, our results indicate that the marginal benefit of increasing size typically outweighs the marginal benefit of decreasing spacing.

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Appendix A. Analyses conducted with different life history parameters

The results of the dispersal-per-recruit model depend on FLEP level relative to CRT, the distribution of habitat, the mean larval dispersal distance of the species (Kaplan et al., 2006), and the home range length (Moffitt et al., 2009). Specific life history parameters must be used in order to calculate FLEP from fishing mortality (*F*), and in the main analyses we used parameters for black rockfish. In order to show that the results of our analyses are not sensitive to these specific life history parameters, we also conducted the same analyses for cabezon (*Scorpaenichthys marmoratus*), a species with different life history parameters, including a shorter life span and a different fecundity function (Table A1).

We analyzed the fraction of movement combinations that were persistent for combinations of MPA size and spacing at several different levels of exploitation rate outside MPAs (Figs. A1 and A2).

Table A1
Scorpaenichthys marmoratus (cabezon) life history parameters used to generate FLEP in Appendix A analyses.

Parameter	Value	Definition	Source
L_∞	62.12	Asymptotic von Bertalanffy length (cm)	Cope et al. (2005)
k	0.18	von Bertalanffy growth parameter	Cope et al. (2005)
t_0	−1.06	Age at which individual would be length 0	Cope et al. (2005)
a_{mat}	3	Age at 50% maturity	Cope et al. (2005)
Max age	15	Maximum age	Love (1996)
d	9.2×10^{-6}	Coefficient in weight at length (kg)	Cope et al. (2005)
b	3.187	Exponent in weight at length	Cope et al. (2005)
M	0.25	Natural mortality rate (uncertain estimate)	Cope et al. (2005)
t_c	3	Age at first capture in fishery	We chose this to correspond with a_{mat}
*Eggs(in 1000's) = (f * weight) + g*			
f	15.3	Parameter in weight–fecundity relationship	O'Connell (1953)
g	27.3	Parameter in weight–fecundity relationship	O'Connell (1953)

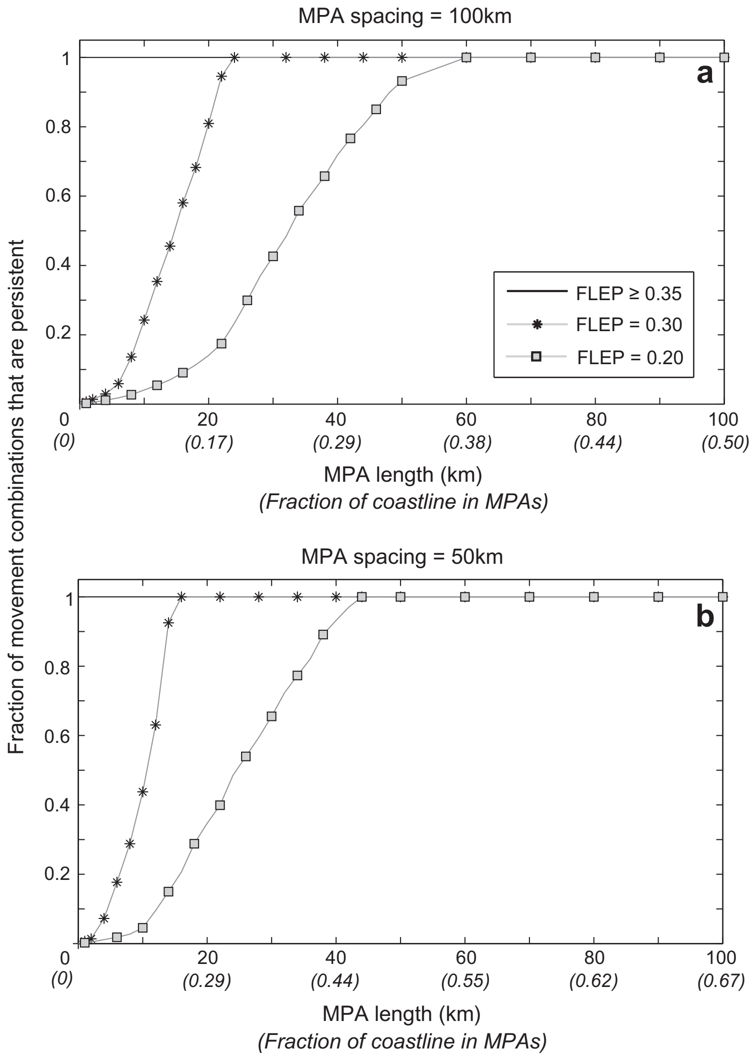

Fig. A1. The fraction of larval dispersal and home range combinations persistent (e.g., the shaded area of persistent populations in Fig. 2) in a network of MPAs of a given length, spaced 100 km (a) and 50 km (b) in an infinite coastline with continuous habitat. Mean larval dispersal distances and home range lengths in the set span 0–100 km and 0–40 km, respectively. Results for FLEP values of 0.20, 0.30, and ⩾0.35 are plotted. The fraction of the coastline in MPAs is also shown. Extraneous data points were removed from the plots to improve clarity.

With the age at first capture set to that of the age at 50% maturity and for the given fecundity relationship, cabezon could not be fished below a FLEP level of 0.16. For this reason, results are only given for FLEP levels of 0.20, 0.30 and ⩾0.35. We first show the effects of MPA size, with spacing held constant at 100 km or 50 km (Fig. A1). The results are very similar to Fig. 3 in the main text, which are derived using black rockfish life history parameters. The relationship between MPA size and the fraction of persistent

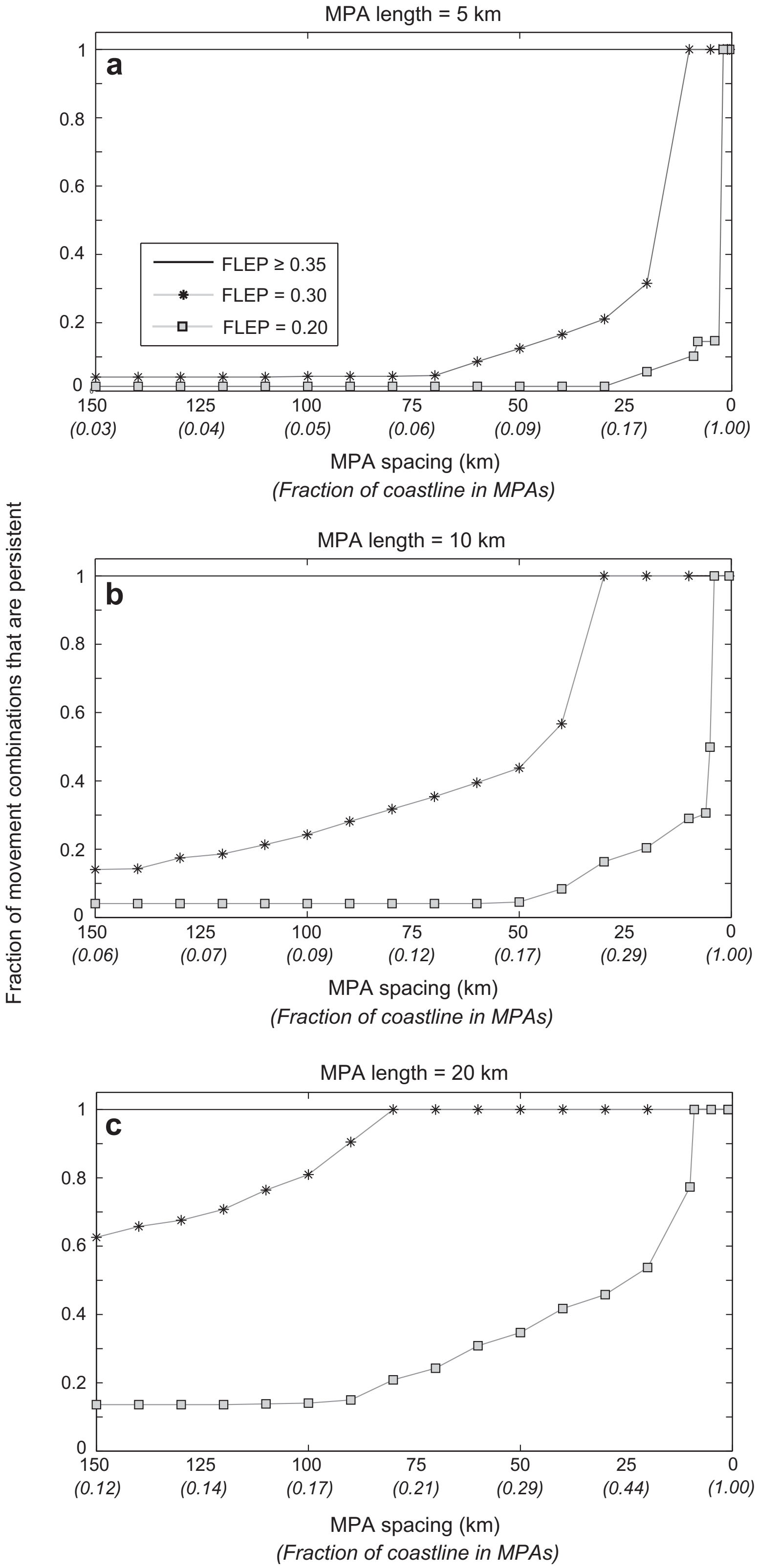

Fig. A2. The fraction of larval dispersal and home range combinations persistent in a network of 5 km (a), 10 km (b), and 20 km (c) MPAs for an array of MPA spacing in an infinite coastline with continuous habitat. Mean larval dispersal distances and home range lengths in the set span 0–100 km and 0–40 km, respectively. Results for FLEP values of 0.20, 0.30, and ⩾0.35 are plotted. The fraction of the coastline in MPAs is also shown. Extraneous data points were removed from the plots to improve clarity.

movement combinations was generally sigmoidal: the marginal benefit of making MPAs larger initially increased with MPA size, and gradually leveled off as the fraction of persistent movement combinations approached 100%. The results did not change greatly between 50 and 100 km spacing, but did depend on the FLEP level outside MPAs. As populations became less overfished (FLEP increased), more movement combinations were persistent. When FLEP was greater than the CRT of 0.35, all movement combinations were persistent with or without MPAs.

In keeping with the main analysis, we also examined the effects of decreasing spacing on the fraction of movement combinations that were persistent for 5, 10, and 20 km long MPAs (Fig. A2). The results are very similar to Fig. 4 in the main text, which are derived using black rockfish life history parameters. Again, the fraction of persistent movement combinations depended greatly on exploitation rate (FLEP) outside MPAs. Decreasing spacing from large values did not lead to persistence for a greater fraction of movement combinations until a certain threshold spacing was reached, at which point increases in the fraction of persistent movement combinations started to occur rapidly.

Comparing results derived from life history parameters from black rockfish (a long-lived species) with those derived from cabezon (a shorter-lived species with a different fecundity function) shows that the general results of our analyses are not specific to the life history parameters used to calculate FLEP.

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