

Accurate assessment of marine protected area success depends on metric and spatiotemporal scale of monitoring

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Supplement 1. Description of the spatial population model and parameter values

Here we provide the equations governing the dynamics of our model. The model is similar to that used by White & Rogers-Bennett (2010) and this description is largely drawn from that paper.

Within-patch model dynamics

We implemented a discrete time, spatially explicit, age-structured, single-species model of a typical rocky reef species. A typical rocky reef species is usually thought of as a life history consisting of a widely dispersing larval phase, settlement to adult habitat, density-dependent post-settlement mortality, a sedentary adult stage with a home range, and iteroparous reproduction without a spawning migration, using either broadcast spawning or benthic egg-laying. We incorporated von Bertalanffy growth, a nonlinear length-weight relationship, and fecundity proportional to biomass. Adults spawn pelagic larvae during an annual reproductive period, larvae disperse according to a dispersal matrix, and settling larvae experience density-dependent survival following a Beverton-Holt survivorship function. The model is summarized by the following equations, taking $\mathbf{N}_j(t)$ to be the vector of abundances of each of A age classes in spatial cell j (out of n total cells) at time t . The number of larval settlers (S) arriving at cell i is

$$S_i(t) = \sum_{j=1}^n D_{ij} f(\mathbf{N}_j(t)) \quad (\text{S1})$$

where D_{ij} is the i, j th element of the dispersal matrix \mathbf{D} and gives the probability of larvae dispersing from j to i . The scalar $f(\mathbf{N}_j)$ is the total fecundity of the population at j :

$$f(\mathbf{N}_j(t)) = SSB_j(t)b \quad (\text{S2a})$$

$$SSB_j(t) = [p(1)B(1), p(2)B(2), \dots p(3)B(A)] \times \mathbf{N}_j(t) \quad (\text{S2b})$$

where \times represents vector multiplication, $SSB_j(t)$ is spawning stock biomass, b is fecundity per unit biomass, $p(a)$ is the probability of being reproductively mature at age a (assumed to be 0 for $a < a_m$ and 1 for $a \geq a_m$), a_m is the age at maturity, and $B(a)$ is mean biomass at age a . Biomass is a function of length, $B(a) = qL(a)^r$, where q and r are constants. Length at age is given by a von Bertalanffy function with growth rate k , age at length zero a_0 , and asymptotic maximum length L_∞ :

$$L(a) = L_\infty [1 - e^{-k(a-a_0)}] \quad (\text{S3})$$

Note that for simplicity we assume there is no variability in length or biomass at age.

The updating step for the population is given by

$$\mathbf{N}_j(t+1) = \begin{bmatrix} 0 \\ e^{-(M+\hat{F}_j(1))} \\ e^{-(M+\hat{F}_j(2))} \\ \vdots \\ e^{-(M+\hat{F}_j(A-1))} \\ 0 \end{bmatrix} \times \mathbf{N}_j(t) + \begin{bmatrix} \frac{\alpha S_j(t)}{1 + \frac{\alpha}{\beta} S_j(t)} \\ 0 \\ \vdots \\ 0 \end{bmatrix} \quad (\text{S4})$$

Note that the initial age class in $\mathbf{N}_j(t+1)$ is comprised of settlers $S_j(t)$ that survive Beverton-Holt density-dependent mortality (with density-independent survivorship α and asymptotic maximum settler density β). Post-settlement individuals have density-independent mortality rate M and experience fishing rate $\hat{F}(a)$, which is a function of age such that $\hat{F}(a) = 0$ for all $a < a_c$, the age at which individuals recruit to the fishery; $\hat{F}(a)$ is constant for all $a \geq a_c$ and was varied to create different fishing scenarios (fishery mortality typically depends on length not age; because our model has deterministic growth, length and age are directly related by Eq. (3), so age a_c corresponds to a particular length). Demographic parameter values were taken from literature estimates for black rockfish *Sebastes melanops* (Table S1).

In this model, generation time T_{gen} (the average age of reproduction) is calculated as

$$T_{\text{gen}} = \frac{\sum_{a=1}^A p(a) B(a) \exp(-Ma) a}{\sum_{a=1}^A p(a) B(a) \exp(-Ma)} \quad (\text{S5})$$

which is simply the product of survival to each age (in the absence of fishing) times reproductive output at each age, times age, divided by the total lifetime reproductive output. To obtain different values of T_{gen} , we adjusted both a_m and M to obtain the desired T_{gen} value.

Calculation of fishing rates

The persistence of an age-structured population with density-dependent recruitment requires that at low population densities, each individual produces on average at least one successful offspring within its lifetime (Hastings & Botsford 2006). Assuming that population density is low enough to ignore density-dependent factors, White (2010) showed that this requirement can be expressed as

$$\alpha \lambda_{\mathbf{D}} \text{FLEP} \geq 1 \quad (\text{S6})$$

where $\lambda_{\mathbf{D}}$ is the leading eigenvalue of the dispersal matrix \mathbf{D} and FLEP is the fraction of unfished lifetime egg production, calculated as the sum of the product of survival to age a and fecundity at age a over all ages A . The basic effect of fishing is to reduce FLEP (see further details in White et al. 2010). Therefore the persistence threshold in Eq. (S6) can be expressed as

$$\text{FLEP} \geq 1 / \alpha \lambda_{\mathbf{D}} \quad (\text{S7})$$

The quantity $1/\alpha \lambda_{\mathbf{D}}$ is referred to as the Critical Replacement Threshold (CRT). The CRT is mathematically related to the Goodyear compensation ratio and the steepness parameter, both of which are often used in fisheries models (White 2010); the CRT is interpreted as the minimum FLEP required for population persistence. In order to keep our analysis general—rather than specific to black rockfish—we express fishing effort in terms of the FLEP it produces, and parameterize α so that $\text{CRT} = 0.25$ in all model runs. In this way, the level of fishing is expressed relative to the persistence threshold, and results would be similar across species for the same value of FLEP relative to CRT.

Larval dispersal

We modeled a case of a 100 km linear coastline consisting of one hundred 1 km wide cells. Thus \mathbf{D} is a 100×100 matrix giving the probability of larval dispersal between each pair of cells. We assumed a

spatial domain consisting of a linear coastline with homogenous habitat. We assumed that demographic parameters were constant across all 100 spatial cells and that the fishing rate, F , was also constant across space (except that $F = 0$ inside any marine protected area [MPA]).

Dispersing larvae (and adult home ranges, see next section) wrapped around the edge of the domain, eliminating edge artifacts and making the coastline effectively infinite (very similar results would be obtained on a very long non-infinite coastline, but our approach is computationally much simpler). In principle, model results should be sensitive to this assumption; if the domain had absorbing boundaries then a species with long larval dispersal distances should lose many larvae off of the edge of the domain. This would result in lower overall larval replenishment and make it less likely that the species would persist. However, as described above, the model is parameterized such that the persistence threshold is precisely given by Eq. (S6), regardless of losses due to larval survival or transport processes. Therefore, we have avoided any sensitivity to assumptions about domain boundaries. Larval dispersal was assumed to be purely diffusive and described by a Gaussian dispersal kernel with zero mean displacement and a standard deviation d_L .

Adult movement

Adult fish can move inside home ranges, so fish that settle inside MPAs can move across MPA boundaries and experience fishing pressure. We assumed that home range movement follows a Gaussian distribution with mean 0 and standard deviation d_H , so that fish spend 95% of their time within a radius $2d_H$ of their settlement location (cf. Freiwald 2009, Moffitt et al. 2009). Then the fishing pressure for a fish with home range centered at spatial cell j is given by

$$\hat{F}_j = \frac{1}{d_H \sqrt{\pi/2}} \int_{-\infty}^{\infty} c_x F_x \exp\left[-\frac{4(x-x_0)^2}{d_H^2}\right] dx \quad (\text{S8})$$

where \hat{F} is the effective fishing rate experienced by an individual with a home range centered at spatial cell j , \hat{F}_x is the fishing rate at location x , $c_x = 0$ for reserves and 1 for fished areas, and x_0 is the center of cell j , and the integration is made over one-dimensional space x . The effective fishing rate \hat{F}_j was then used to calculate FLEP _{j} and the expected fishery yield of recruits settling at each cell j . This is similar to the approach taken by Moffitt et al. (2009), but with a Gaussian rather than uniform distribution of home range movement.

Parameter values used

Table S1 shows the general parameter values that were used in the \hat{F} model runs. Table S2 shows parameter values specific to the fishing scenarios.

Table S1. *Sebastes melanops*. Parameter values used in model. Notation follows White & Rogers-Bennett (2010)

Parameter	Value	Definition
A	30	Maximum age (yr)
a_c	4	Age at first capture in fishery (yr)
a_m	6, 8, 13	Age at maturity (yr) ^a
M	0.774, 0.18, 0.1	Natural mortality rate (yr ⁻¹) ^a
Beverton-Holt settler–recruit curve		
$R = \alpha S / (1 + (\alpha/\beta)S)$		
α	220.99, 2.13, 1.17	Density-independent survival (slope at origin) ^b
β	1	Maximum settler density (fish area ⁻¹)
Length-at-age (cm)		
$L(a) = L_\infty \{1 - \exp[-k(a - a_0)]\}$		
L_∞	44.2	Asymptotic length (cm)
k	0.33	von Bertalanffy growth parameter (yr ⁻¹)
a_0	0.75	Age at length 0 (yr)
Weight-at-length (kg)		
$W = pL^q$		
p	1.68×10^{-5}	Coefficient (kg)
q	3	Exponent

^a a_m and M were adjusted to produce generation times of 7, 13, and 19 yr, respectively.
^bThe slope parameter was fitted to achieve a Goodyear compensation ratio of 4, given other life history parameters. Different values were required for each generation time.

Table S2. Fishing scenarios used in the model for simulations with each value of generation time, T_{gen} . FLEP = fraction of lifetime egg production

	T_{gen}					
	7 yr		13 yr		19 yr	
	FLEP	F	FLEP	F	FLEP	F
F_{low}	0.7477	0.0997	0.7404	0.0350	0.7427	0.0201
F_{med}	0.3727	0.3594	0.3654	0.1283	0.3677	0.0702
F_{high}	0.1250	0.8129	0.1250	0.2991	0.1250	0.1540

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Supplement 2. Analysis with alternative species parameter values

In the main text we presented results using demographic parameters for black rockfish *Sebastes melanops*. In order to check the robustness of those results we repeated the analysis using parameters for cabezon *Scorpaenichthys marmoratus*, another nearshore California fish (Table S3).

When results were scaled by appropriate spatial and temporal values, results for *Scorpaenichthys marmoratus* were extremely similar to those for *Sebastes melanops*, at least in terms of the spatial and temporal scales of population responses. The patterns of population density over space after implementation (Figs. S1 & S2 for Cases 1 and 2, respectively) showed the same types of gradients over the same distance from the reserve edge as in *S. melanops* (compare to Figs. 2 & 3 in the main text). The patterns of inside versus outside and after versus before ratios were also similar to the corresponding results for *S. melanops* (we only simulated F_{med} conditions in *S. marmoratus* for both Case 1 and Case 2; for *S. marmoratus* life history parameters $F_{\text{med}} = 0.60$ [corresponding to FLEP = 0.45], and generation time $T_{\text{gen}} = 7.3$ yr) in terms of the time scale of response (asymptotic equilibrium has been reached or at least long-term trajectory is evident after 1 to 2 generations; compare Fig. S3 to Figs. 4 & 5 in the main text). As with *S. melanops*, there were some scenarios in which the after versus before ratio decreased while the inside versus outside ratio increased or remained constant (Fig. S3c,d).

Table S3. *Scorpaenichthys marmoratus*. Parameter values used in model. Notation follows White & Rogers-Bennett (2010)

Parameter	Value	Definition
A	13	Maximum age (yr)
a_c	4	Age at first capture in fishery (yr)
a_m	3	Age at maturity (yr)
M	0.25	Natural mortality rate (yr^{-1})
T_{gen}	7.3	Generation time (yr) ^a
Beverton-Holt settler–recruit curve		
$R = \alpha S / (1 + (\alpha/\beta)S)$		
α	1.29	Density-independent survival (slope at origin) ^b
β	1	Maximum settler density (fish area^{-1})
Length-at-age (cm)		
$L(a) = L_{\infty} (1 - \exp(-k(a - a_0)))$		
L_{∞}	62.12	Asymptotic length (cm)
k	0.18	von Bertalanffy growth parameter (yr^{-1})
a_0	-1.06	Age at length 0 (yr)
Weight-at-length (kg)		
$W = pL^q$		
p	9.2×10^{-6}	Coefficient (kg)
q	3.187	Exponent

^aThis is the natural generation time (Eq. S5 from Supplement 1), given literature estimates of the other model parameters

^bThe slope parameter was fitted to achieve a Goodyear compensation ratio of 4, given other life history parameters

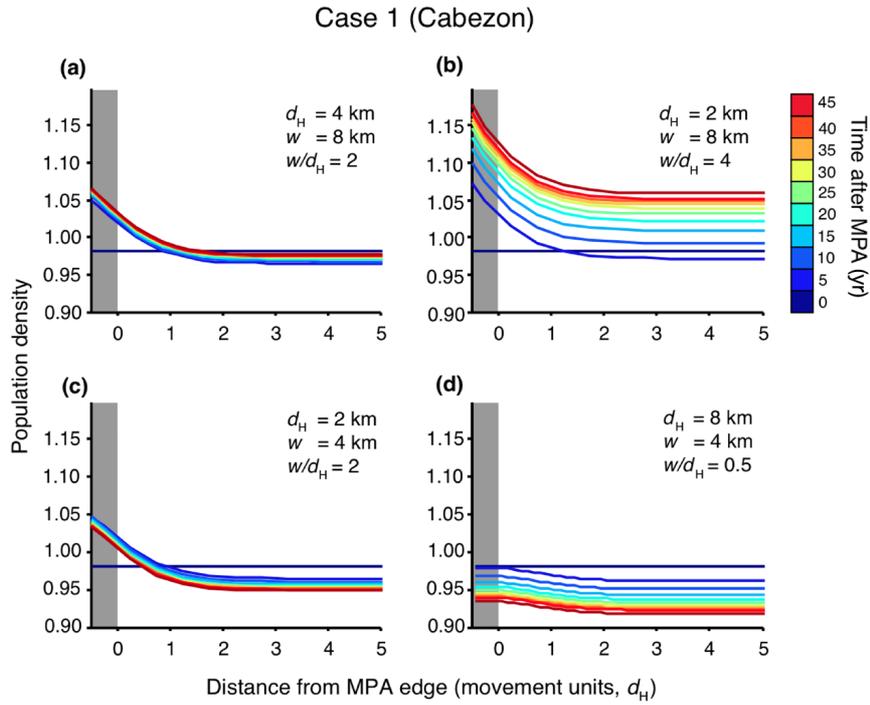


Fig. S1. *Scorpaenichthys marmoratus*. Spatial patterns of population density in Case 1 (long larval dispersal [$d_L = 100$ km], varying home range size) with fishing mortality rate F_{med} and a range of home range distances (d_H) and marine protected area (MPA) widths (w). Curves show population density in 5 yr increments after MPA implementation; color indicates time. Gray shading indicates location of MPA. Distance from MPA edge is scaled to units of home range distance (d_H). Note that the dark blue horizontal line denotes population density at time 0

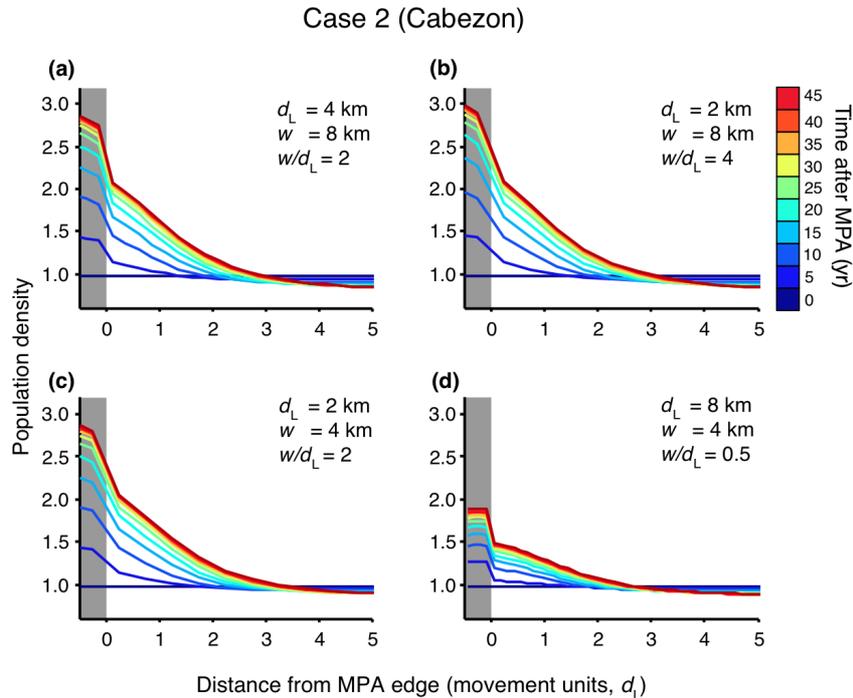


Fig. S2. *Scorpaenichthys marmoratus*. Spatial patterns of population density in Case 2 (short home range [$d_H = 0.01$ km], varying larval dispersal distances) with fishing mortality rate F_{med} and a range of larval dispersal distances (d_L) and marine protected area (MPA) widths (w). Curves show population density in 5 yr increments after MPA implementation; color indicates time. Gray shading indicates location of MPA. Distance from MPA edge is scaled to units of larval dispersal distance (d_L). Note that the dark blue horizontal line denotes population density at time 0

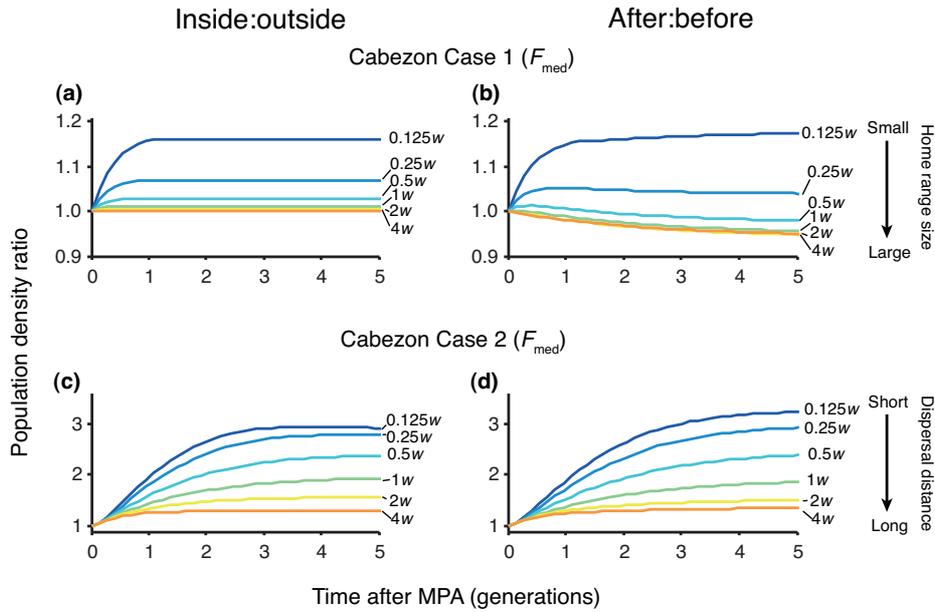


Fig. S3. *Scorpaenichthys marmoratus*. Response over time after marine protected area (MPA) implementation. In (a, c), population density is shown as the inside versus outside response ratio ([density at the center of the MPA]/[density at the location $3 d_H$ from the MPA edge]) in year t . In (b, d), population density is shown as the after versus before response ratio at the center of the MPA. Results are shown for F_{med} and (a, b) Case 1 (long d_L [100 km], varying d_H), (c, d) Case 2 (short d_H [0.01 km], varying d_L). Each curve corresponds to a different value of d_H (Case 1) or d_L (Case 2); d values are expressed relative to MPA width; here $w = 8$ km. Time is expressed as generation time of the species (here $T_{gen} = 7.3$ yr)

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White JW, Rogers-Bennett L (2010) Incorporating physical oceanographic proxies of recruitment into population models to improve fishery and marine protected area management. CalCOFI Report 51:128–149

Supplement 3. Exploring the consequences of additional fishing scenarios

In the main text we presented results for representative values of marine protected area (MPA) width ($w = 4$ km), fisherman behavior ($s = 0$), and fishing scenarios ($F = F_{\text{med}}$). Here we explore the consequences of choosing different values for those parameters.

Exploring the consequences of fishing rate on the effect of MPAs over space

In Figs. 2 & 3 in the main text we showed how population density changed over space in the years following MPA implementation for $F = F_{\text{med}}$ and selected values of w , d_H , and d_L . These general effects and their spatial scale are consistent across different values of those parameters, although the magnitude of the MPA effects on population density increases with fishing mortality rate (Figs. S4 & S5). In Case 1 (long larval dispersal distance and varying home range size), the maximum inside versus outside ratio is consistently found beyond 3 home range units (d_H) from the MPA edge in Year 5 (Fig. S4a,c,e). Plotting the after versus before ratio in Year 5 for each location outside the MPA reveals that there is no change in population density due to the MPA beyond 3 d_H units (Fig. S4b,d,f). Additionally, the magnitude of changes in population density across space is inversely related to home range size (d_H) (Fig. S4). Similar patterns hold for Case 2 (short home range and varying larval dispersal), in which magnitude and spatial scale of the MPA effect over space are functions of larval dispersal distance (d_L) (Fig. S5).

Exploring the consequences of varying fisherman behavior and MPA width

The behavior of the fishing fleet is described as such: given a total fishing effort F_T , in each year the fleet allocates effort based on the previous year's distribution of catchable biomass, B to the $i = 1, 2, \dots, n$ model cells:

$$F(t, i) = F_T \frac{B(t-1, i)^s}{\sum_{j=1}^n B(t, j)^s} \quad (\text{S9})$$

The parameter s determines how sensitive fishing effort is to the spatial distribution of fish. For $s = 0$, effort is even across space. For $s = 1$, fishing is highest at the MPA edge where biomass is spilling over from the MPA ('fishing the line'); this effect is more extreme with $s = 10$. Simulations in the main text had values of $s = 0$. We show results over time with $s = 1$ and $s = 10$ for Case 1 (Figs S6 & S8) and Case 2 (Figs. S7 & S9) using both inside versus outside ratios (at a distance of $3d$ from the MPA edge; Figs. S6 & S7) and after versus before ratios (for the center of the MPA; Figs. S8 & S9). In these figures we also show results for MPA widths of both $w = 4$ km (as shown in the main text figures) and $w = 8$ km.

While varying s did produce slight variations in the overall magnitude of the inside versus outside and after versus before ratios, it did not alter the basic patterns with respect to d , w , and F (Figs. S6 to S9). With $s = 10$ and F_{high} , there was some year-to-year variability in the fishing pattern and thus the inside versus outside ratio as the fleet moved in response to exponentially declining stocks outside the MPA; nonetheless the general patterns remained consistent despite this variability (Figs. S6i & S7i). In general, the value of F had the greatest overall effect on the temporal trend and spatial pattern of abundance after MPA implementation. Additionally, simulations with different MPA widths (w) but the same ratio of d/w had nearly identical patterns (curves with the same d/w ratio are aligned in the key legend of Figs. S6 to S9; note that in most cases these curves overlap considerably in the figures), supporting the conclusion that spatial patterns of abundance beyond the MPA edge are a consistent function of the d/w ratio.

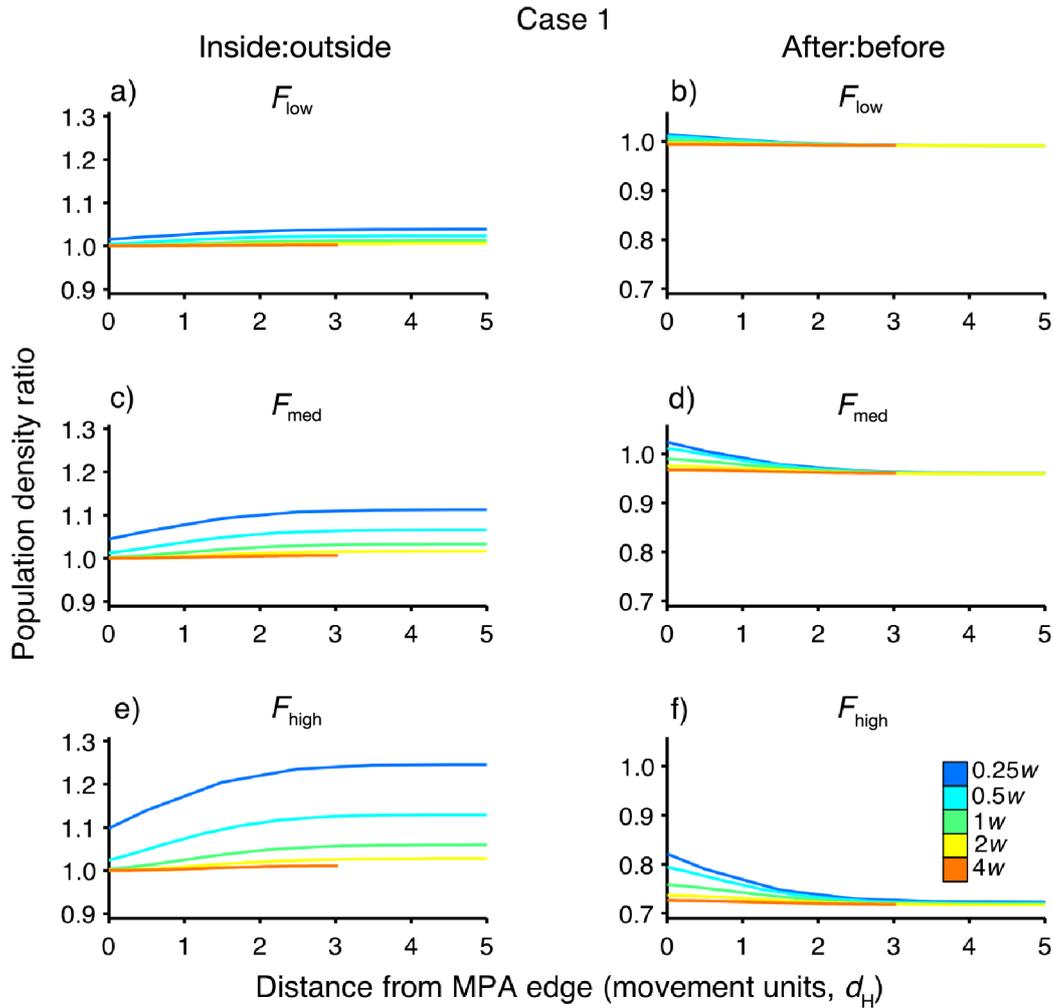


Fig. S4. Population response over space 5 yr after marine protected area (MPA) implementation for Case 1 (long distance larval dispersal and varying home range size). For (a, c, e), population density is shown as the inside versus outside response ratio of (density at the center of the MPA)/(density at the location d_H units from the MPA edge). For (b, d, f), population density is shown as the after versus before response ratio of (density at a given distance from the MPA edge in Year 5)/(density at the same location in Year 0). Results are shown for fishing rates of (a, b) F_{low} , (c, d) F_{med} , and (e, f) F_{high} . Each curve corresponds to a different value of d_H (expressed relative to MPA width, w ; $w = 4$ km in simulations shown here). Distance from the MPA edge is also expressed in terms of d_H . Note that results for $d_H = 4w$ are only shown up to $3d_H$ (48 km) from the MPA edge, which is the midpoint of the 100 km repeating coastline unit

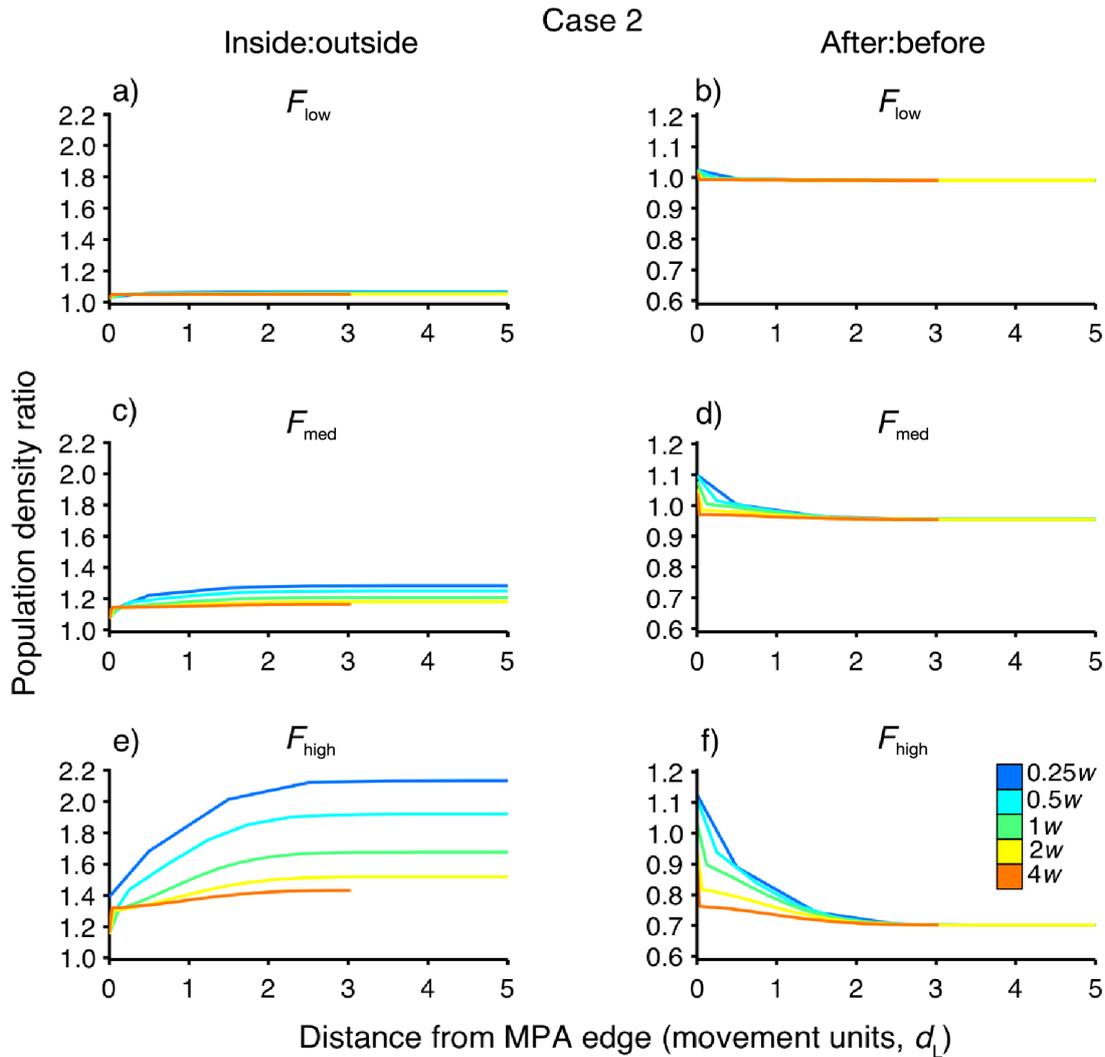


Fig. S5. Population response over space 5 yr after marine protected area (MPA) implementation for Case 2 (short home range distance and varying larval dispersal distance). For (a, c, e), population density is shown as the inside versus outside response ratio of (density at the center of the MPA)/(density at the location d_L units from the MPA edge). For (b, d, f), population density is shown as the after versus before response ratio of (density at a given distance from the MPA edge in Year 5)/(density at the same location in Year 0). Results are shown for fishing rates of (a, b) F_{low} , (c, d) F_{med} , and (e, f) F_{high} . Each curve corresponds to a different value of d_L (expressed relative to MPA width, w ; $w = 4$ km in simulations shown here). Distance from the MPA edge is also expressed in terms of d_L

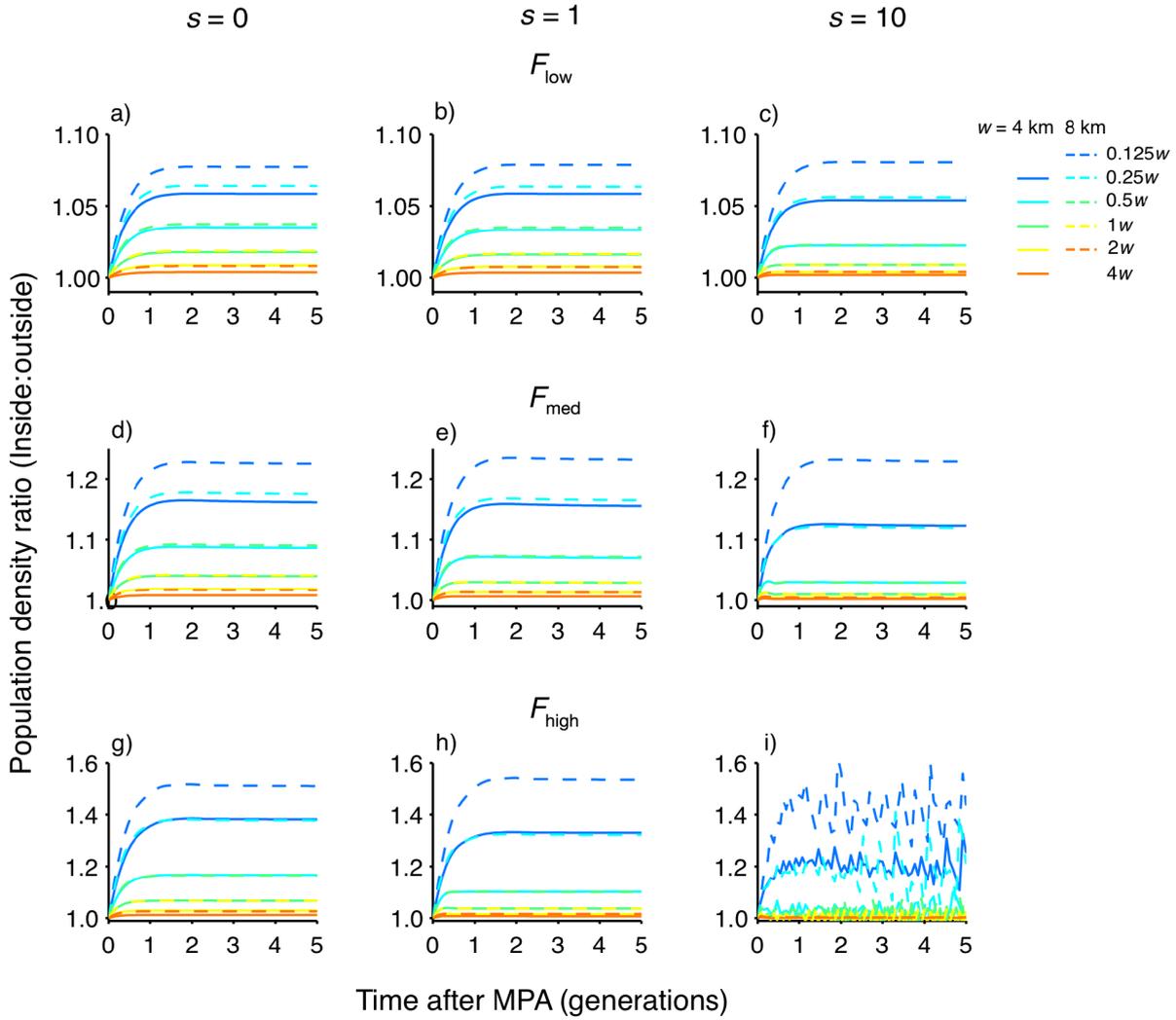


Fig. S6. Population response over time after marine protected area (MPA) implementation for Case 1 (long distance larval dispersal and varying home range size). Population density is shown as the inside versus outside response ratio of (density at the center of the MPA in year t)/(density at the location 3 home range distance units (d_H) from the MPA edge in Year t). Results are shown for fishing rates of (a, b, c) F_{low} , (d-f) F_{med} , and (g, h, i) F_{high} and fisherman movement parameters of (a, d, g) $s = 0$, (b, e, h) $s = 1$, (c, f, i) $s = 10$. Each curve corresponds to a different value of d_H (expressed relative to MPA width (w) and indicated by color) and MPA width (indicated by line style). Identical line color indicates cases in which d_H values are equal. Time is expressed relative to the generation time, T_{gen} , of the species ($T_{gen} = 13$ yr in simulations shown here). Note that vertical axis scale varies among panels

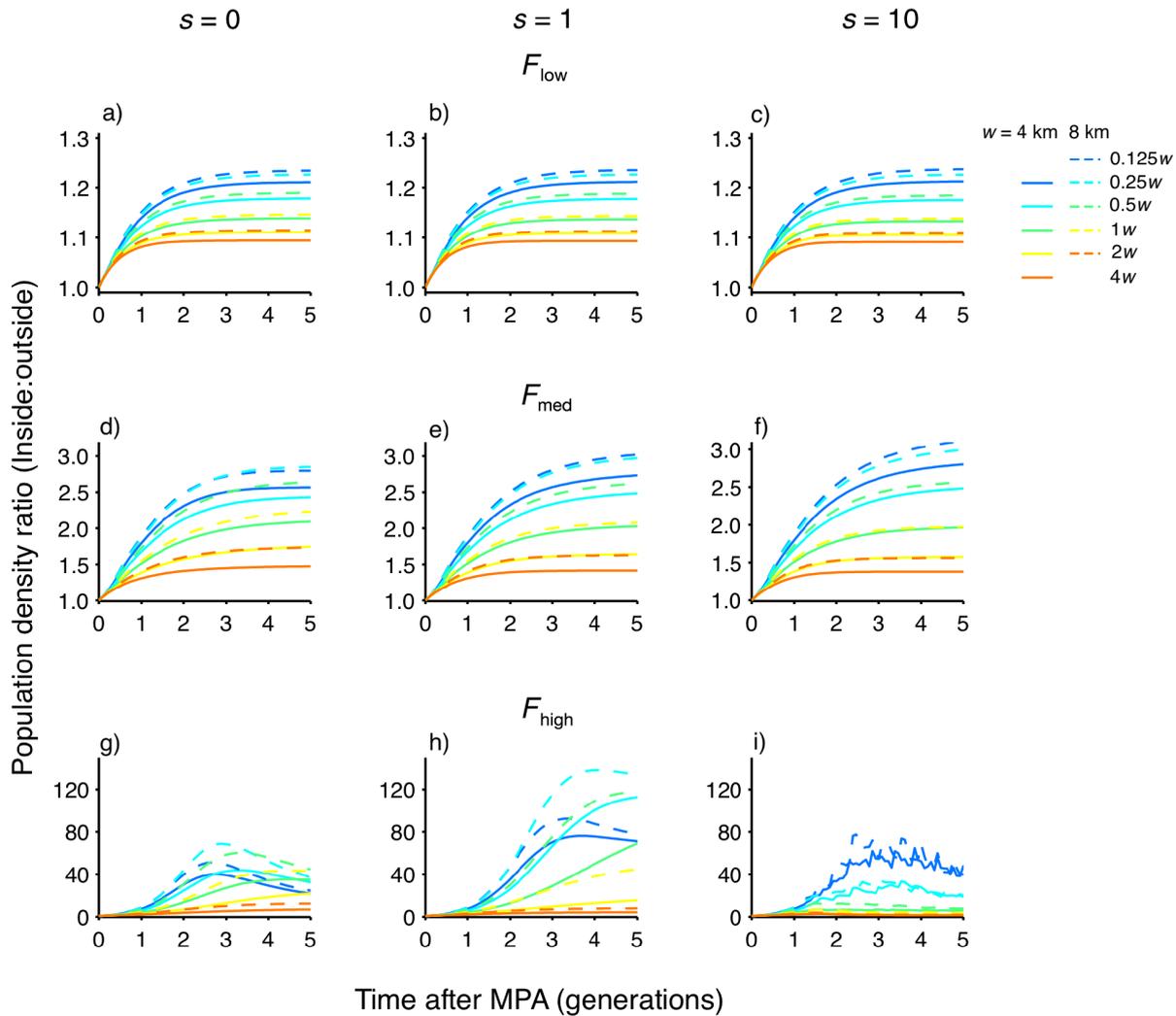


Fig. S7. Population response over time after marine protected area (MPA) implementation for Case 2 (short home range distance and varying larval dispersal distance). Population density is shown as the inside versus outside response ratio of (density at the center of the MPA in year t)/(density at the location 3 larval dispersal distance units (d_L) from the MPA edge in Year t). Results are shown for fishing rates of (a, b, c) F_{low} , (d, e, f) F_{med} , and (g, h, i) F_{high} and fisherman movement parameters of (a, d, g) $s = 0$, (b, e, h) $s = 1$, (c, f, i) $s = 10$. Each curve corresponds to a different value of d_L (expressed relative to MPA width, w , and indicated by color) and MPA width w (indicated by line style). Time is expressed relative to the generation time, T_{gen} , of the species ($T_{gen} = 13$ yr in simulations shown here). Note that vertical axis scale varies among panels

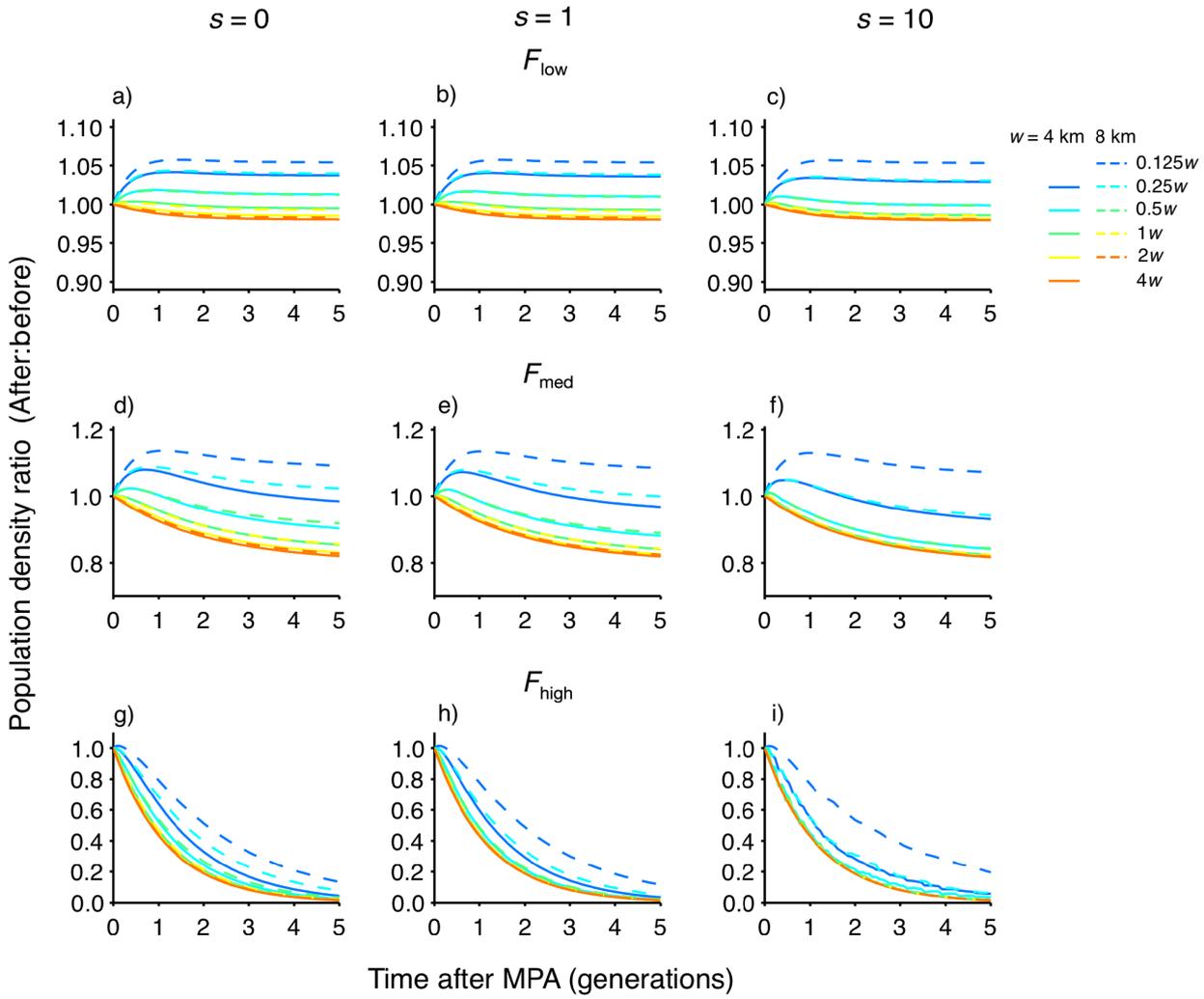


Fig. S8. Population response over time after marine protected area (MPA) implementation for Case 1 (long distance larval dispersal and varying home range size). Population density is shown as the after versus before response ratio of (density at the center of the MPA in Year t)/(density at the center of the MPA in Year 0). Results are shown for fishing rates of (a, b, c) F_{low} , (d, e, f) F_{med} , and (g, h, i) F_{high} and fisherman movement parameters of (a, d, g) $s = 0$, (b, e, h) $s = 1$, (c, f, i) $s = 10$. Each curve corresponds to a different value of d_H (expressed relative to MPA width, w , and indicated by color) and MPA width w (indicated by line style). Time is expressed relative to the generation time, T_{gen} , of the species ($T_{gen} = 13$ yr in simulations shown here). Note that vertical axis scale varies among panels

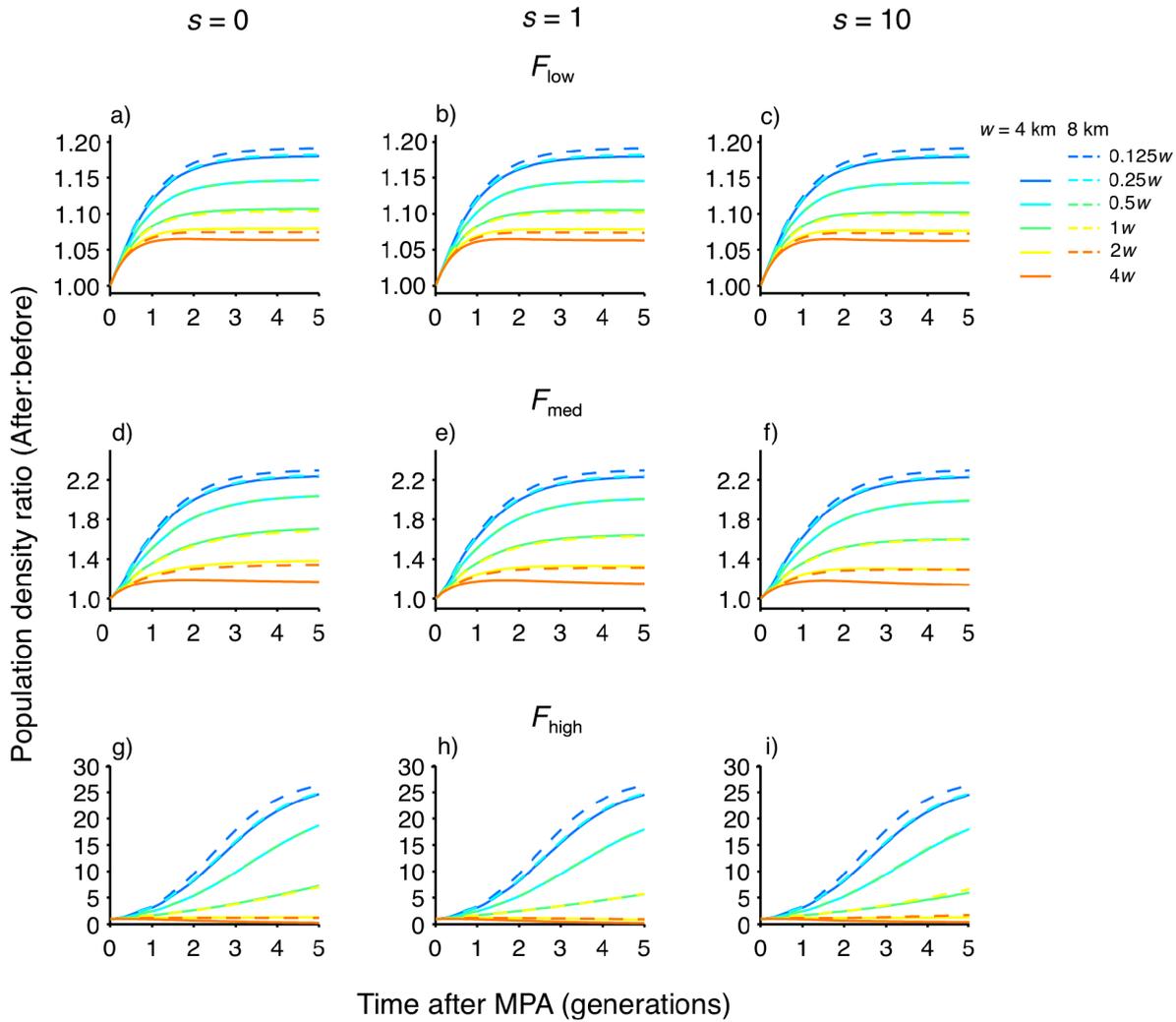


Fig. S9. Population response over time after marine protected area (MPA) implementation for Case 2 (short home range distance and varying larval dispersal distance). Population density is shown as the after versus before response ratio of (density at the center of the MPA in year t)/(density at the center of the MPA in Year 0). Results are shown for fishing rates of (a, b, c) F_{low} , (d, e, f) F_{med} , and (g, h, i) F_{high} and fisherman movement parameters of (a, d, g) $s = 0$, (b, e, h) $s = 1$, (c, f, i) $s = 10$. Each curve corresponds to a different value of d_L (expressed relative to MPA width, w , and indicated by color) and MPA width w (indicated by line style). Time is expressed relative to the generation time, T_{gen} , of the species ($T_{gen} = 13$ yr in simulations shown here). Note that vertical axis scale varies among panels