

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

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ABSTRACT: Marine protected areas are being monitored to determine whether they increase abundance of fished populations, with responses often expected within a few years. Evaluations typically compare abundance inside versus outside or after versus before implementation, but the temporal and spatial scales over which these measures can reflect marine protected area success are untested. We modeled the response of fished populations for a range of marine protected area sizes, fishing intensities, larval dispersal distances, and adult movement ranges. Our results, which can inform experimental design and interpretation of monitoring, show that the spatial and temporal scale of population responses to marine protected areas will be determined by simple relationships between marine protected area size, larval and adult movement distances, and generation time, in addition to the effects of exploitation rate. The largest effects of marine protected areas should be expected with 'outside' samples located at least 2 dispersal units from the edge, and after 2 generations have passed since establishment. In general, monitoring studies over time (after versus before) should provide better assessment of marine protected area success than monitoring over space (inside versus outside), but understanding of the limitations of each type of measurement is key. Because it may take many years for marine protected area effects to be fully realized, we strongly caution against judgment of marine protected area effectiveness at inappropriately short time frames.

KEY WORDS: Ecosystem-based management · Fisheries · Monitoring · Population dynamics · Transient dynamics · Larval dispersal · Movement · Marine reserve

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INTRODUCTION

Marine protected areas (MPAs), ocean locations where at least some extractive activities are prohibited, are being established worldwide to achieve conservation and management goals (Lester et al. 2009). Monitoring programs are often employed to determine whether MPAs meet their intended goals (Hamilton et al. 2010, McCook et al. 2010). While ecological theory provides general expectations for factors affecting MPA success over long time scales (reviewed

by White et al. 2011), we lack general guidelines for the temporal and spatial scales at which the effects of MPAs on fished species could be detected from various measurements. This poses challenges for the design and analysis of MPA monitoring programs.

The effects of MPAs are typically monitored by measuring population variables (e.g. density, biomass) or fisheries variables (e.g. catch). MPAs are expected to increase the abundance of fished species within their boundaries, and it is often also expected that the abundance of fished species will increase outside

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their boundaries as well (hereafter by MPA 'effects' we mean this expected increase in abundance). The ratio of abundance in the MPA after versus before implementation, and the ratio of abundance inside versus outside the MPA after implementation are commonly used as metrics of MPA performance (e.g. Halpern 2003, Harborne et al. 2008, Lester et al. 2009). While there are no formal, theoretically grounded expectations for these metrics of MPA performance, the assumption is often made in MPA evaluations and meta-analyses that positive ratios (either inside versus outside or after versus before) mean an MPA is 'successful' (Claudet et al. 2008, Harborne et al. 2008, Lester et al. 2009). Furthermore, it is often suggested that evaluation of MPA performance should occur as soon as 5 yr after implementation (Halpern & Warner 2002, Gerber et al. 2005, CDFG 2009).

Detecting the effects of MPA implementation on fished populations is a 2-part problem: (1) Is there an effect? (2) Can it be detected? If there is an MPA effect, its detectability depends on how long it takes for the effect to provide adequate contrast for detection. The dynamics of this initial transient response have not been investigated until recently (White et al. 2013a) and are the focus of this paper. Detectability also depends on variability in the response, including measurement error (which we do not address here) and environmental stochasticity (which we have considered elsewhere, see White & Rogers-Bennett 2010).

Previous modeling efforts demonstrate that long-term MPA success is strongly affected by the intensity of fishing effort outside MPA boundaries and by the spatial scales of larval and adult movement of fished species. An individual MPA should have a greater positive effect on a population if fishing effort exceeds the level that would cause population collapse (Holland & Brazee 1996, White et al. 2010a), and if the MPA is large relative to the spatial scale of larval dispersal and/or adult movement (Botsford et al. 2001, Moffitt et al. 2009, White et al. 2010a,b, Grüss et al. 2011). These findings have led to guidelines for MPA design (Gaines et al. 2010, Moffitt et al. 2011). However, empirical tests of these model predictions have produced mixed results. Meta-analyses have found varying responses to MPA establishment: some found positive effects of MPA size (Claudet et al. 2008, Vandeperre et al. 2011) while others did not (Halpern 2003, Guidetti & Sala 2007); some found positive effects of MPA age (Vandeperre et al. 2001, Micheli et al. 2004, Claudet et al. 2008) while others did not (Halpern & Warner 2002, Halpern 2003); and some found overall MPA effects both positive and negative (Halpern 2003, Lester et al. 2009). This vari-

ability in outcomes may be due in part to the mismatch of scales between modeling (long-term) and empirical observations (short-term) (White et al. 2011). It is possible that measuring MPA effects at the proper spatial and temporal scale during the transient response would resolve these discrepancies.

Here we consider the effects of MPA size, fish movement, and fishing intensity on the short term, transient response to MPAs. We focus on the following questions: (1) How rapidly will MPA effects be detectable? (2) How far away from the MPA will they be detectable? (3) How large will the effects be? and (4) How are these factors related to population increase or decline? One of our aims is to test the assumption that a positive inside versus outside or after versus before ratio indicates MPA 'success'. Because all definitions of success rely on at least maintaining a persistent population, that is how we define it here. Our analyses lead to recommendations of when and where to monitor, as well as methods for scaling results to obtain the greatest benefit from MPA monitoring and analysis.

METHODS

We modeled a fish population occupying a linear coastline comprised of discrete spatial cells using a single-species, deterministic, age-structured, discrete-time population model (see Supplement 1 at www.int-res.com/articles/suppl/m489p017_supp.pdf for model equations and parameter values). Single-species models are not only a necessary first step to understanding population dynamics, they have also been found to be valid representations of population dynamics for individual species in communities with generalist predators (Murdoch et al. 2002). Briefly, adult fish grow asymptotically in length, and fecundity is proportional to biomass. The adult subpopulation in each cell spawns larvae that disperse to other cells according to a dispersal kernel, and settling larvae experience intra-cohort density-dependent mortality. Adults experience density-independent mortality and, after they enter the fishery, fishing mortality. The larval dispersal kernel (the probability of settlement at each location for larvae spawned in a given model cell) is a normal distribution with mean of zero and a standard deviation referred to as the 'larval dispersal distance', d_L (Fig. 1a). Fish that settle within a particular model cell may move beyond that model cell in a fixed home range as adults. We previously found that model results are not highly sensitive to the distribution of the home range (Moffitt et

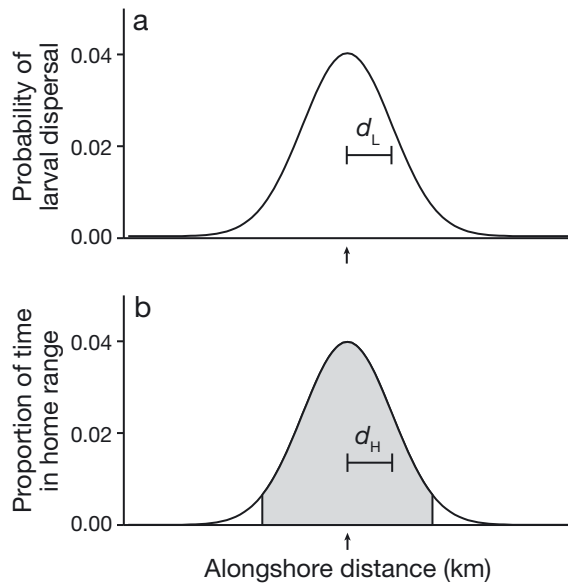


Fig. 1. Movement distance measurements used in this paper. (a) Probability distribution ('dispersal kernel') describing the probability of larval settlement at various distances from the spawning site (vertical arrow). The kernel (solid line) represents diffusive movement, with standard deviation d_L (the 'larval dispersal distance'). (b) Probability distribution describing the proportion of time an adult spends at various distances from the home range center (vertical arrow). The gray shaded area indicates the 95% confidence region (the 'home range' as typically described in the literature); the scale bar indicates the home range distance d_H , the standard deviation of that distribution

al. 2009). In order to better represent the shapes of home ranges measured by acoustic tracking, we assumed that home range behavior could be described by a normal distribution giving the proportion of time an individual fish spends in each neighboring model cell. Such home range distributions are typically described in terms of the area in which the fish spends $\geq 95\%$ of its time (Lowe & Bray 2006), so we described home range sizes using the 'home range length' d_H , which is the standard deviation of the home range probability distribution (the 95% home range area falls within $1.96d_H$ of the center of the home range; Fig. 1b). Consequently, both larval and adult movements are described by a length scale d , the standard deviation of a normal distribution. We used life history parameter estimates for black rockfish *Sebastes melanops* (Table S1 in Supplement 1). White et al. (2013a) used an analytical model to show that generation time (defined as the average age of reproduction) is the dominant demographic factor affecting the time scale of transient population responses to MPAs. Therefore, we varied the natural mortality rate and age at maturity to mimic genera-

tion times, T_{gen} , for shorter and longer generations compared to the natural value of $T_{gen} = 13$ yr in order to investigate how generation time affects the time scale of the MPA response. We varied the parameters a_m (age at maturity, yr) and M (natural mortality rate, yr^{-1}), so that T_{gen} took on values of 7, 13, and 19 yr. To further test the generality of our results, we conducted the same analysis using cabezon *Scorpaenichthys marmoratus*, a fish with very different demographic parameters (Supplement 2 at www.int-res.com/articles/suppl/m489p017_supp.pdf).

We started all model runs at unfished equilibrium, then ran the model forward 50 yr with a constant fishing rate. An MPA was then introduced into the center of the domain and the model was run for an additional 200 yr. Total fishing effort was kept constant within each model run and redistributed outside of the MPA after establishment. In order to avoid idiosyncratic edge effects, the model domain (one hundred 1 km wide cells) was made circular (i.e. larval dispersal and home range movement wrapped around the edge). We made model runs with MPAs of width $w = 4$ km and $w = 8$ km, and show how results are generalizable to other widths. Because abundance (in numbers) is a common measure reported in MPA monitoring studies and a goal for both biodiversity and fisheries MPAs, we chose population density ratios (inside versus outside and after versus before) as our measure of MPA effects. Examining biomass was another option, but it confounds changes in abundance with changes in size structure.

Given the strong effect of the fishing rate outside MPAs on equilibrium MPA performance (White et al. 2010a), we considered 3 different fishing mortality rates, chosen based on their population dynamic effects. The settler-recruit curve was parameterized with a compensation ratio of 4; that is, the population will persist if lifetime egg production (LEP) is 25% of the unfished value (we refer to this as the fraction of unfished LEP, i.e. FLEP; White 2010). For the demographic parameters we used, maximum sustainable yield (MSY) occurred when FLEP was approximately 50%. To illustrate a range of responses to fishing we ran simulations with fishing rates that produced FLEP values of 12.5% (high fishing, F_{high} ; halfway between the collapse point and FLEP = 0), 37% (moderate fishing, F_{med} ; halfway between the collapse point and MSY), and 75% (low fishing, F_{low} ; halfway between MSY and the unfished state). In the long run, populations with F_{high} would collapse, while populations with F_{med} and F_{low} would reach nonzero equilibrium abundances. The values of F corresponding to each FLEP level depended on the

generation time, T_{gen} (Table S2 in Supplement 1). We show results for fishing effort that is uniformly distributed outside the MPA. Because spatial variation in fishing effort is known to be important (Kellner et al. 2007) we also made simulations in which fishing effort followed the abundance of fish biomass to varying degrees, although this did not affect the general results (Supplement 3 at www.int-res.com/articles/suppl/m489p017_supp.pdf).

Results of earlier equilibrium analyses (e.g. Moffitt et al. 2009, White et al. 2010b), informed our initial focus on the consequences of home range and larval movement on short-term MPA effects using 2 cases. These cases correspond to the 2 forms of population persistence in MPA networks: a single MPA may be 'self persistent' (i.e. large enough to support a self-sustaining subpopulation without outside input), or a group of non-self-persistent MPAs may be 'network persistent' if they exchange a sufficient number of larvae among themselves each generation (Botsford et al. 2001, Hastings & Botsford 2006, White et al. 2010b). In general, self-persistence under intensive fishing requires that the MPA be larger than the larval dispersal distance, d_L (Botsford et al. 2001, White et al. 2010b). In Case 1, the population had long larval dispersal distance ($d_L = 100$ km), with a range of home range sizes, d_H equal to 1, 2, 4, 8, and 16 km, which range from quite small to larger than the 2 MPA widths. Thus, only network persistence would be possible in Case 1. In Case 2, the population had home range movement small enough to be negligible ($d_H = 0.01$ km), and larval dispersal distance was varied over a range of values: d_L equal to 1, 2, 4, 8, and 16 km. Case 2 included larval dispersal distances in which self-persistence was possible ($d_L \leq w$) and those in which only network persistence was possible ($d_L > w$). Additionally, we simulated additional movement combinations of d_L and d_H ranging from $0.01w$ to $4w$ in order to show how a realistically wide range of movement scales can be understood in terms of the 2 cases that we investigated in depth.

RESULTS

Changes in population density after MPA implementation exhibited spatial and temporal patterns that differed across a range of dispersal distances and MPA sizes. For example, a species with a larger home range showed population density effects due to MPA implementation farther from the MPA edge than a species with a small home range (Moffitt et al.

2009). In the results shown here, we scaled distance from the MPA edge by dividing distance by either larval dispersal distance (d_L) or home range (d_H) to obtain a nondimensional distance ratio. This allowed direct comparison of patterns across dispersal distances and illustrated the generality of results.

Changing effects over space

In Case 1 (long larval dispersal, varying home range), changes in population density after MPA implementation exhibited spatial and temporal patterns that depended on dispersal distance relative to MPA size and time since implementation (Fig. 2). For $F = F_{\text{med}}$ and home range distances smaller than the MPA width ($d_H < w$), fish density initially increased inside the MPA, then declined somewhat towards the long-term equilibrium; at the same time, density declined steadily outside the MPA (Fig. 2a–c). Note that the population was not at equilibrium when the MPA was implemented (it was still declining from the initial unfished state). Consequently, the long-term equilibrium density was often lower than the density at the time of implementation.

The maximum difference in density between inside versus outside the MPA was found $>2d_H$ from the MPA edge. The inside versus outside gradient was present over that $2d_H$ spatial scale from soon after MPA implementation until equilibrium; this result was consistent across all levels of fishing, fisherman behaviors, and MPA widths, although fishing intensity did affect the equilibrium density (see Supplement 3). A similar gradient also appeared for larger home range sizes ($d_H > w$), although population density decreased both inside and outside the MPA in that situation (Fig. 2d).

In Case 2 (short home range, varying larval dispersal), changes in population density after MPA implementation also exhibited a range of different spatial and temporal patterns that depended on dispersal distance relative to MPA size and time since implementation (Fig. 3). For $F = F_{\text{med}}$, fish density increased gradually within the MPA and declined at points distant from the MPA. The spatial gradient in density from inside to outside MPA increased gradually as the system moved towards the new, post-MPA equilibrium. This gradient was nearly identical for values of d_L shorter than MPA width (Fig. 3a–c) and very similar for d_L greater than MPA width, although the inside to outside gradient was smaller in the latter (Fig. 3d). Because biomass from larval spillover gradually accumulated outside the MPA, the distance at

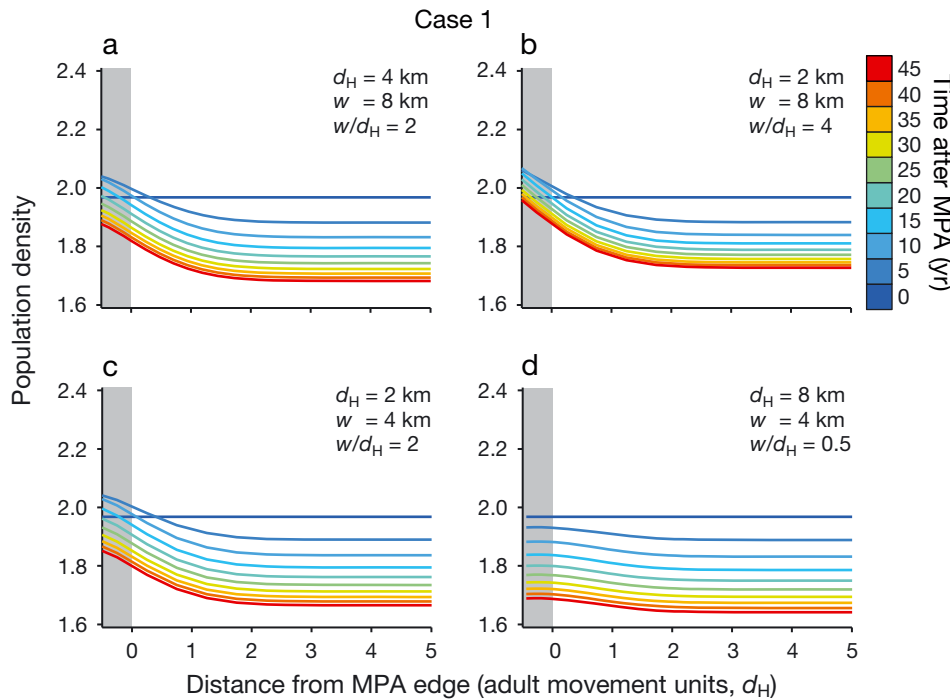


Fig. 2. Spatial patterns of population density in Case 1 (long larval dispersal [$d_L = 100$ km], varying home range) with fishing mortality rate F_{med} and a range of home range distances (d_H) and marine protected area (MPA) widths (w). Curves show population density in 5 yr increments after MPA implementation; 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

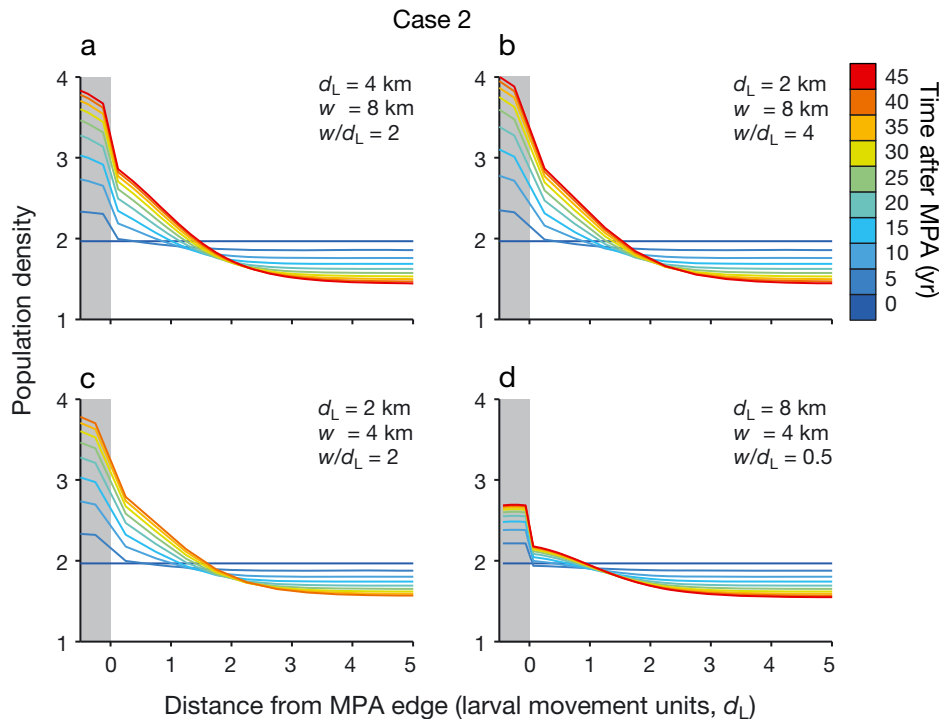


Fig. 3. Spatial patterns of population density in Case 2 (short home range [$d_H = 0.01$ km], varying larval dispersal) with fishing mortality rate F_{med} and a range of larval dispersal distances (d_L) and marine protected area (MPA) widths (w). Curves show population density in 5 yr increments after 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

which the inside to outside difference was greatest gradually increased over time, and at equilibrium was >3 dispersal distance units from the MPA edge. This result was consistent across all levels of fishing, so long as the population actually increased inside

the MPA (Supplement 3). The population density decreased inside the MPA only when the fishing rate was unsustainable (F_{high}) and d_L was too large relative to w for the MPA to be self-persistent (this scenario is not shown in Fig. 3 but is shown in Fig. 5).

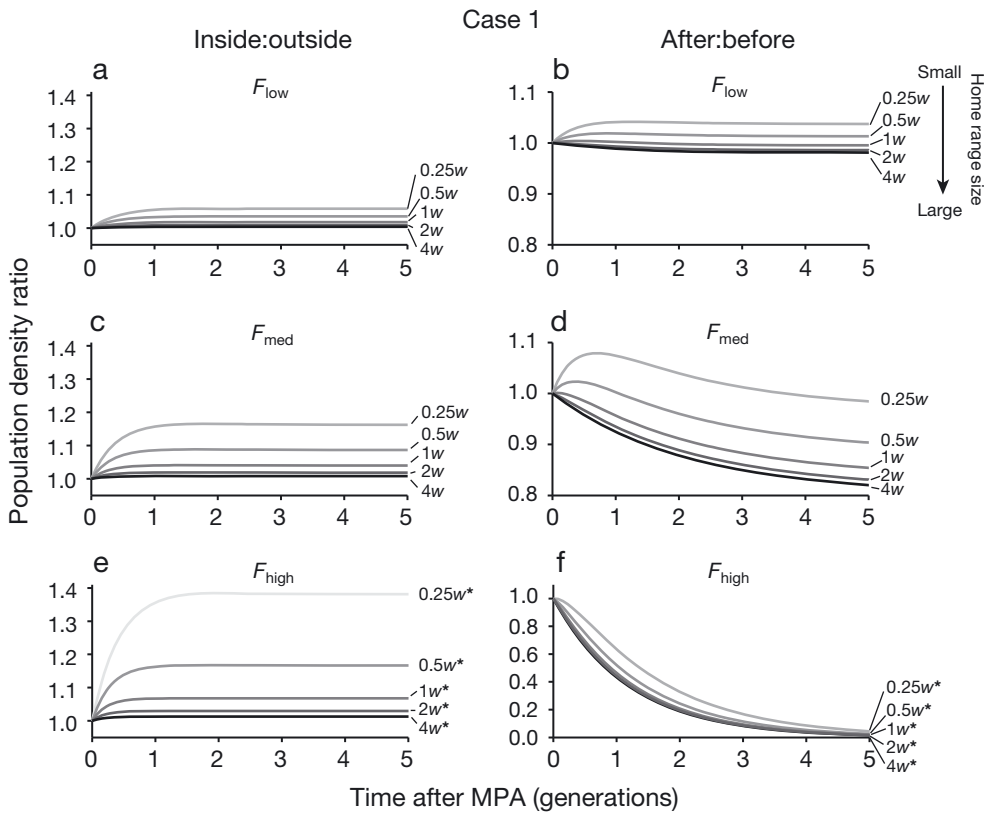


Fig. 4. Response over time after marine protected area (MPA) implementation for Case 1 (long larval dispersal [$d_L = 100$ km]), varying home range). For (a,c,e), population density is shown as the inside versus outside response ratio ([density at the center of the MPA]/[density at the location $3 d_H$ from the MPA edge]) in year t . For (b,d,f), population density is shown as the after versus before response ratio at the center of the MPA. Results are shown for (a,b) F_{low} , (c,d) F_{med} , and (e,f) F_{high} fishing rates. Each curve corresponds to a different value of d_H (expressed relative to MPA width; here $w = 4$ km). Time is expressed as generation time of the species (here $T_{gen} = 13$ yr). Asterisks (*) indicate populations that eventually decline to extinction

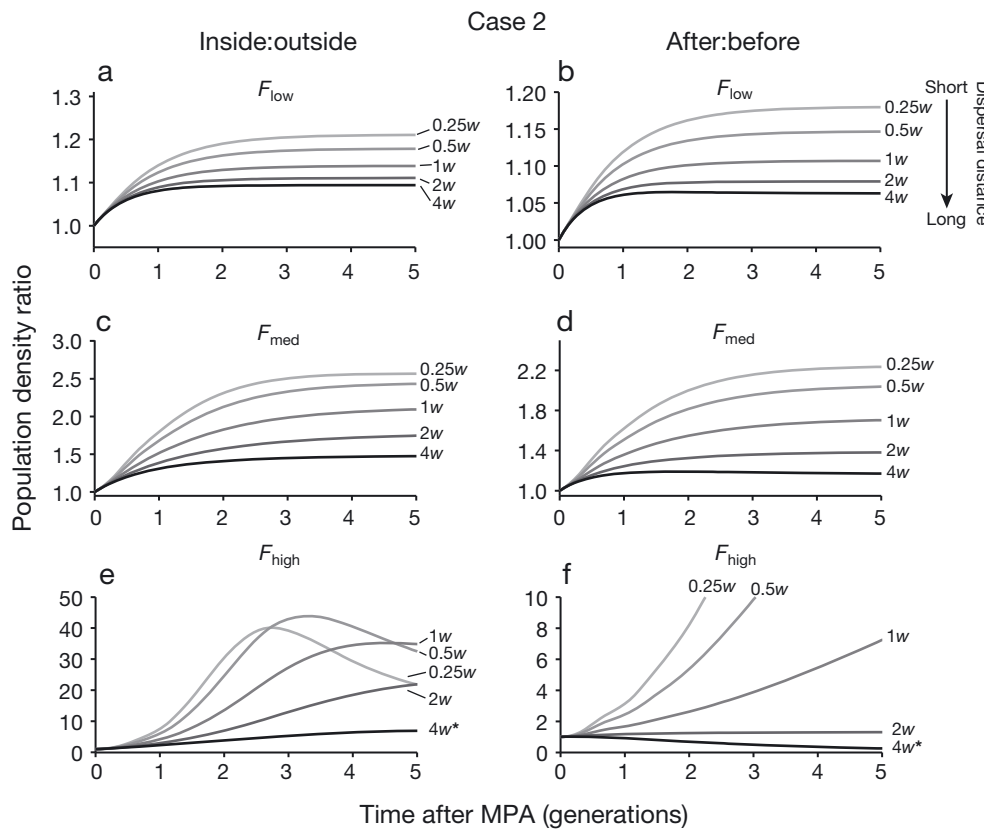


Fig. 5. Response over time after marine protected (MPA) implementation for Case 2 (short home range [$d_H = 0.01$ km]), varying larval dispersal). For (a,c,e), population density is shown as the inside versus outside response ratio ([density at the center of the MPA]/[density at the location $3 d_H$ from the MPA edge]) in year t . For (b,d,f), population density is shown as the after versus before response ratio at the center of the MPA. Results are shown for (a,b) F_{low} , (c,d) F_{med} , and (e,f) F_{high} fishing rates. Each curve corresponds to a different value of d_L (expressed relative to MPA width; here $w = 4$ km). Time is expressed as generation time of the species (here $T_{gen} = 13$ yr). Asterisks (*) indicate populations that eventually decline to extinction

Inside versus outside ratios over time

Figs. 2 & 3 suggest that the closest monitoring location to detect the largest possible inside versus outside ratio (or close to the largest ratio; the ratio increases asymptotically) after MPA implementation is at 3 movement units (d_H in Case 1 or d_L in Case 2) from the MPA edge. To see how the inside versus outside ratio calculated at a distance of $3d$ would change over time, we calculated the ratio using the population density of the cell in the center of the MPA ('inside') and the population density in the cell $3d$ from the MPA edge ('outside') over time (scaled by generation T_{gen}) (Figs. 4 & 5). The shape of that trajectory was nearly identical for simulations that had different MPA widths (w) and movement distances (d_H , d_L) but had the same ratio of w to d (Supplement 3). Therefore in Figs. 4 & 5 we show only results for $w = 4$ km and express d as a proportion of w .

For Case 1 (long larval dispersal, varying home range), the inside versus outside ratio was 1 at time zero (there was no difference prior to the MPA) and reached its maximum after approximately 2 generations (Fig. 4a,c,e). The shapes of the temporal patterns of the responses were consistent across fishing and home ranges, as long as time was scaled by generation time. The magnitude of the ratio was greater for smaller home ranges (because there was less spillover from the MPA into fished areas), with greater differences among home range sizes for higher fishing rates because higher fishing led to lower fish abundances outside of the MPA. Note that the inside versus outside ratio reached a constant positive value even at F_{high} , a level of fishing at which the population was declining to zero (compare Fig. 4e,f). In other words, a positive and constant inside versus outside ratio was not indicative of a sustainable population.

For Case 2 (short home range, varying larval dispersal), the inside versus outside ratio also plateaued after approximately 2 to 3 generations, with a few exceptions (Fig. 5a,c,e). For the highest fishing rate and dispersal distances shorter than MPA width ($d_L \leq w$), the inside versus outside ratio actually peaked and declined to a slightly lower equilibrium value after 3 generations (Fig. 5e). This occurred because the 'inside' density increased monotonically to a maximum while the 'outside' density initially decreased, then increased when the spillover front (seen in Fig. 2) reached the $3d_L$ monitoring location. The increase due to spillover to the $3d_L$ monitoring location was slightly greater and more rapid for shorter dispersal distances, which caused the inside

versus outside ratio to peak and level out to the equilibrium somewhat faster.

After versus before ratios over time

When we expressed MPA effects over time as the ratio of population density at the center of the MPA after versus before MPA implementation, results were once again equivalent for simulations with the same ratio of w to d (Supplement 3). Therefore we show only the results for $w = 4$ km and express d relative to w (Figs. 4 & 5).

For Case 1 (long larval dispersal, varying home range), the trend in after versus before ratios represented the behavior of the whole population much better than inside versus outside ratios. Whereas the inside versus outside ratio rapidly reached a stable value regardless of the overall population trajectory (e.g. despite a gradual decline, Fig. 4e–f), the after versus before ratio only stabilized after the population reached equilibrium. This occurred after 1 to 2 generations for the lowest fishing rate (Fig. 4b). Under F_{med} and F_{high} , however, population density gradually declined to a lower equilibrium (Fig. 4d) or to extinction (Fig. 4f) even for some instances in which there was an initial increase inside the MPA. In these 2 instances the long-term equilibrium was not reached within 3 generations, but within 1 to 2 generations the population trajectory was declining in the direction of the equilibrium.

For Case 2 (short home range, varying larval dispersal), the trend in after versus before ratios (Fig. 5b,d,f) was also broadly similar to that of the inside versus outside ratios in the sense that shorter larval dispersal distances were associated with greater ratios. The clearest difference was that for the highest fishing rate and larval dispersal distances that were smaller than the MPA width ($d_L \leq w$), the after versus before ratio took 10 to 12 generations to reach its asymptotic maximum (Fig. 5f). For longer dispersal distances ($d_L > w$) under F_{high} , the MPA was not self-persistent and the after versus before ratio gradually declined to zero, as in Case 1 (Fig. 4f).

Exploring the effects of generation time

The results shown in Figs. 4 & 5 were scaled to the generation time of the model species (13 yr). To examine the effect of variability in generation time on those results, we also explored T_{gen} values of 7 and 19 yr. We then examined the temporal trend in the

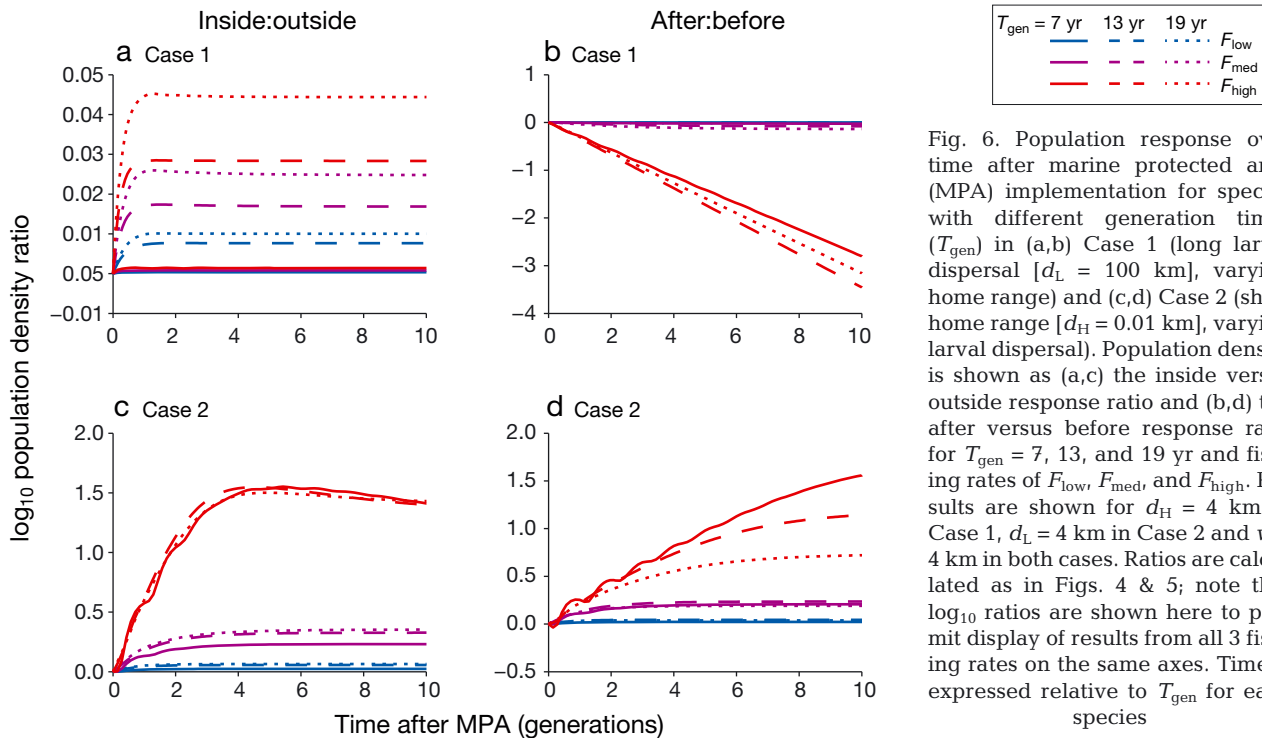


Fig. 6. Population response over time after marine protected area (MPA) implementation for species with different generation times (T_{gen}) in (a,b) Case 1 (long larval dispersal [$d_L = 100$ km], varying home range) and (c,d) Case 2 (short home range [$d_H = 0.01$ km], varying larval dispersal). Population density is shown as (a,c) the inside versus outside response ratio and (b,d) the after versus before response ratio for $T_{\text{gen}} = 7, 13,$ and 19 yr and fishing rates of $F_{\text{low}}, F_{\text{med}},$ and F_{high} . Results are shown for $d_H = 4$ km in Case 1, $d_L = 4$ km in Case 2 and $w = 4$ km in both cases. Ratios are calculated as in Figs. 4 & 5; note that \log_{10} ratios are shown here to permit display of results from all 3 fishing rates on the same axes. Time is expressed relative to T_{gen} for each species

inside versus outside and after versus before ratio of population density in the center of the MPA, using the scenario in which movement distances equal MPA width as an example (Fig. 6; $d_H = d_L = w = 4$ km). For both Cases 1 and 2, populations with different generation times but the same fishing rate (relative to FLEP) exhibited similar trajectories in inside versus outside and after versus before ratios as a function of generation time (Fig. 6). While simulations with different T_{gen} values had different final equilibria, the rate of approach to equilibrium was similar when expressed in terms of T_{gen} . The curves also exhibited oscillations with a period approximately equal to T_{gen} at the highest fishing rate in Case 2; the amplitude of these oscillations is higher for short T_{gen} and so are only visible for $T_{\text{gen}} = 7$ yr (Fig. 6d; note that similar oscillations are present but very subtle in Fig. 5d).

Additional spatial scales of movement

The simulations in Case 1 and Case 2 illustrate a range of parameter values that produce consistent results when scaled to movement distance (d_H or d_L). However, other combinations of d_H and d_L are also likely. Furthermore, if d_H and d_L are similar in magnitude (e.g. not a very large larval dispersal distance as in Case 1 or a very small home range as in Case 2),

it is not clear whether the spatial gradient in the inside versus outside density ratio would scale with d_H , d_L , or some combination of the 2. Therefore we performed additional simulations (using the same model parameter values as Figs. 2 to 5) in which we varied both d_H and d_L simultaneously, including 961 combinations of the 2 parameters, each ranging over 31 values from $0.00125w$ to $4w$, using $w = 8$ km and $F = F_{\text{med}}$ (Fig. 7).

Earlier we showed how the inside versus outside ratio reached an asymptotic maximum at a consistent scaled distance from the MPA edge ($2d_H$ in Case 1 [Fig. 2] and $3d_L$ in Case 2 [Fig. 3]). In order to characterize the position of that asymptote in our additional simulations, we calculated the distance at which the inside versus outside ratio was one-half of the maximum asymptotic distance at $t = 40$ yr after MPA implementation. In Cases 1 and 2, this half-maximum distance $d_{1/2}$ occurred at close to 1 movement unit from the MPA edge (Figs. 2 & 3). Therefore we calculated the absolute value of the difference between $d_{1/2}$ and 3 values: d_H , d_L , and $d_H + d_L$. Here we used the sum of the 2 movement scales ($d_H + d_L$) as another simple scaling option. The value with the smallest absolute difference would be the one that best explains the spatial scale of the inside versus outside gradient for that simulation.

Comparing the absolute difference between $d_{1/2}$ and d_H (Fig. 7a), d_L (Fig. 7b), and $d_H + d_L$ (Fig. 7c), we

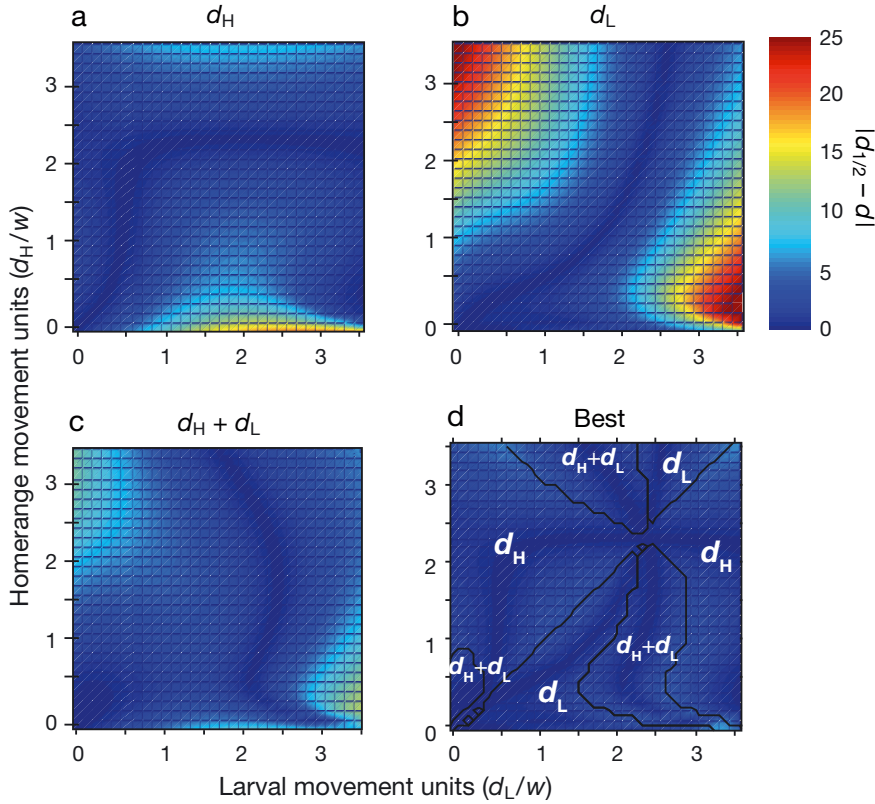


Fig. 7. Spatial scale of the population response to marine protected area (MPA) implementation for different combinations of adult movement scale d_H and larval movement rate d_L with fishing mortality rate F_{med} and MPA width (w) of 8. Panels (a,b,c) show the absolute value of the difference between the distance at which the inside versus outside ratio of population density is one-half the maximum ($d_{1/2}$, estimated at $t = 40$ yr after MPA implementation and indicated by color) and (a) d_H , (b) d_L , or (c) $d_H + d_L$. Panel (d) shows the minimum difference possible for each simulation, and the contour lines indicate which of the 3 measures of movement scale affords the best scaling for the inside versus outside ratio. Movement units are expressed relative to w

found that each value afforded good scaling (low absolute difference) for some combinations of d_H and d_L but not others. In Fig. 7d, for each movement combination we show the minimum absolute differences found in any of the panels (a), (b) and (c) (i.e. Fig. 7d shows the bluest regions compared to the other 3 panels). The contour lines demarcate regions in which a particular metric provides the best scaling for each combination of d_H and d_L . For most values of d_H and relatively small values of d_L , the half-maximum distance scaled with whichever movement scale is greater. For example, in Case 2 (short home range, varying larval dispersal), d_L was always much greater than d_H and results scaled best with d_L (the values of d_H and d_L used in Case 2 would all fall along the horizontal axis of Fig. 7d, where d_L is the better scaling metric). Once d_L became very large ($>3w$), d_H provided better scaling because self-persistence within the MPA is no longer possible. This is true for the examples in Case 1 (long larval dispersal, varying home range), which scaled well with d_H and would all fall beyond the right edge of Fig. 7d, where d_H is the best scaling metric. There were also some regions of intermediate d_L for which $d_{1/2}$ scaled best with $d_H + d_L$. Thus the spatial scale of the MPA effect can be predicted by some combination of adult and larval movement scales for any species.

DISCUSSION

We have shown that the spatial and temporal scale of population responses to MPAs were determined by simple relationships between MPA size, larval and adult movement distances, and generation time, in addition to the effects of exploitation. This can inform experimental design and interpretation of monitoring studies using the life histories of the species of interest, and set expectations for targeted, tactical models of specific scenarios. The largest effects of MPAs should be expected with 'outside' samples located at least 2 dispersal units from the MPA edge and after 2 generations have passed since MPA establishment. In general, monitoring studies over time (after versus before) provide better assessment of MPA success (in terms of maintaining a persistent population) than monitoring over space (inside versus outside). This is a key result because the minimum requirement of successful management with MPAs is maintaining a persistent population, and inside versus outside ratios are not a trustworthy indication of this. Our results show that the appropriate scale for MPAs to affect a population is generation time of the species, not chronological time. Because this could imply that many years would be necessary for MPA effects to be fully realized, we

strongly caution against judgment of MPA effectiveness at inappropriately short time frames.

While population density patterns for all movement combinations scaled by movement distance (d_H , d_L , or $d_H + d_L$) and generation time, there were some general differences between the 2 cases. For Case 1 (long larval dispersal, varying home range), both types of movement were large enough to be significant, leading to limited buildup of population density in the MPA (Figs. 2 & 4). In contrast, for Case 2 (short home range, varying larval dispersal), all movement was basically from larval dispersal. The very short home range allowed greater buildup of population density in the MPA, and also allowed the effects of larval spillover to be seen (Figs. 3 & 5).

Empirical studies and meta-analyses measuring the individual effects of MPA size, time since protection, and fish mobility on fish populations within MPAs have yielded mixed results (Côté et al. 2001, Halpern & Warner 2002, Halpern 2003, Micheli et al. 2004, Claudet et al. 2008, Vandeperre et al. 2011). We have shown that the combination of these factors, along with exploitation rate, determines the magnitude (and thus detectability) of MPA effects on density, potentially confounding tests for the effects of a single factor. For example, Micheli et al.'s (2004) meta-analysis found no significant relationship between adult mobility and post-MPA increases in abundance, but mobility was positively correlated with exploitation rate among species. We have shown that while increased mobility should reduce MPA effects, the associated increase in exploitation level would produce the opposite response, suggesting that their test for an effect of mobility may have been confounded by exploitation level. Empirical studies of MPA effects that report the movement of the population relative to MPA size and the level of its exploitation beyond fished versus unfished should have the best ability to interpret their results.

Understanding the limitations of each type of population density measurement after MPA implementation is key to their interpretation. While ecologists usually prefer a full before and after, control versus impact design (BACI) that incorporates both after versus before and inside versus outside information (Osenberg et al. 2011), this is rarely available for studies of MPA effects (Halpern 2003, Claudet et al. 2008, Lester et al. 2009). The MPA effects on population density are most commonly measured by comparing density inside the MPA to density at a control site outside the MPA at one point in time (the inside versus outside ratio, Lester et al. 2009). We have shown that spillover of larval production from the

MPA and the resulting increase in density can reach several multiples of the mean dispersal distance away from the MPA boundaries (for many species tens or hundreds of kilometers away). It is likely that monitoring programs will measure the 'outside' density much closer to the MPA than that, in which case the inside versus outside ratio will underestimate the net difference in density inside compared to a control site further from the MPA. Additionally, the inside versus outside ratio may not increase monotonically; spillover can produce an expanding front of increasing population densities, and the inside versus outside ratio may increase to a maximum then decrease as the spillover front reaches the 'outside' monitoring site (Fig. 5).

Despite their popularity (Lester et al. 2009), measured inside versus outside ratios must be interpreted with caution. The measurement of density inside versus outside an MPA may show greater change (and therefore be more detectable) than a measurement in the center of an MPA before versus after implementation. However, a positive inside versus outside ratio is not diagnostic of population persistence, and can be observed even in declining populations where the MPAs are not enough to secure persistence. In contrast, the after versus before ratio was diagnostic of population persistence, but often exhibited transient dynamics that took up to 2 generations to reach equilibrium (Figs. 4 & 5). In cases in which the approach to equilibrium took longer, it could be determined after 2 generations if the population was increasing or declining (Fig. 5f). This finding adds to the argument that long-term after:before comparisons are an important component of assessing MPA effects (Vandeperre et al. 2011), and serves as caution for using positive inside versus outside ratios as indicators of MPA success. It also suggests that it could be informative to re-examine the data used in meta-analyses to determine which instances with inside density greater than 1.0 may have involved declining populations.

The second approach typically used to detect MPA effects is to compare population density at a single site within the MPA before and after implementation. This approach avoids the problem of determining the appropriate outside control location, but is not without its limitations. For example, under unsustainable fishing rates, population densities inside the MPA might continue to decline after MPA implementation before reaching a non-zero equilibrium (e.g. Fig. 4d). This would produce an after to before ratio of <1 , which could be interpreted as failure of the MPA, despite the fact that the MPA will eventually succeed

in preserving a population — an example of the general principle that short-term transient dynamics may not be representative of the long-term equilibrium outcome (Hastings 2010). Even when the short-term dynamics are similar to the long-term equilibrium, it may take more than a generation for the full effects of the MPA to be realized (Figs. 4 & 5). Given the long lifespans of many temperate fishes protected in MPAs, this result should temper expectations for the rapid realization of MPA effects.

MPA effects are also evaluated by determining whether trajectories of density inside and outside the MPA diverge over time (Hamilton et al. 2010). Careful interpretation is necessary here as well. If the trajectories inside versus outside the MPA do not diverge through time but are parallel, the assumption may be that environmental change is forcing a change in both locations or that the MPA has no effect on density (Harborne et al. 2008). We have shown that trajectories may be parallel simply because the outside comparison site is too close to the MPA and is therefore sampling spillover effects.

Our results show that movement distances and generation times are a fundamental uncertainty of MPA management, and correct estimations of these parameters are key to realistic expectations of MPA performance and subsequent interpretations of whether an MPA is effective. The variance of movement distances and generation times among species suggest that the results of monitoring should be highly dependent on life history. Even for those species for which we have not yet estimated larval dispersal, home range, or generation time precisely, we usually know at least the order of magnitude of these parameters. These can be used as a first cut for interpretation of MPA monitoring data; a marked improvement from the status quo of ignoring their effect.

There are several caveats regarding the use of the results presented here. First, we represented the dynamics of the coastline using a deterministic model, but the stochasticity inherent in natural systems should further obscure the ability to detect MPA effects (White & Rogers-Bennett 2010). We represented larval dispersal with a symmetric dispersal kernel for generality of results, but the specific directional hydrodynamics of the area of interest would also be important to consider (Gaines et al. 2003). Second, MPAs are often being designed and implemented to function as an interconnected network (Fernandes et al. 2005, Kaplan et al. 2009, White et al. 2013b). While we confined our analysis here to the optimistic scenario (with regard to the detectability of MPA effects) of a single MPA in a deterministic system, it is reason-

able to assume that the closer MPAs are to each other, the more homogeneous the variables of interest would be along the coastline and the more difficult it would be to avoid sampling spillover effects. Third, species with high fishing rates, older ages of mortality and lower natural mortality may exhibit oscillatory transient responses, possibly initially declining, even when the ultimate response is positive (White et al. 2013a). Such oscillations were evident in some of our simulations (Figs. 5 & 6), and although we did not focus on that aspect of the results, it affords yet another reason to use caution when calculating after versus before ratios over short time scales.

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