

Habitat-dependent movement rate can determine the efficacy of marine protected areas

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Abstract. Theoretical studies of marine protected areas (MPAs) suggest that more mobile species should exhibit reduced local effects (defined as the ratio of the density inside vs. outside of the MPA). However, empirical studies have not supported the expected negative relationship between the local effect and mobility. We propose that differential, habitat-dependent movement (i.e., a higher movement rate in the fishing grounds than in the MPA) might explain the disparity between theoretical expectations and empirical results. We evaluate this hypothesis by building two-patch box and stepping-stone models and show that increasing disparity in the habitat-specific movement rates shifts the relationship between the local effect and mobility from negative (the previous theoretical results) to neutral or positive (the empirical pattern). This shift from negative to positive occurs when differential movement offsets recruitment and mortality differences between the two habitats. Thus, local effects of MPAs might be caused by behavioral responses via differential movement rather than by, or in addition to, reductions in mortality. In addition, the benefits of MPAs, in terms of regional abundance and fishing yields, can be altered by the magnitude of differential movement. Thus, our study points to a need for empirical investigations that disentangle the interactions among mobility, differential movement, and protection.

Key words: differential movement; fishing harvest; fishing yield; local effect; marine protected area; regional abundance.

INTRODUCTION

Movement strongly influences the distribution of organisms across landscapes and therefore plays a critical role in determining a population's interactions with other species (Mccauley et al. 1996, Hanski 1998, Morales and Ellner 2002, Leibold et al. 2004, Jiao et al. 2016), its response to environmental change (Damschen et al. 2008, Kininmonth et al. 2011, Janin et al. 2012), and the effectiveness of management actions (St. Mary et al. 2000, Starr et al. 2004, Pérez-Ruzafa et al. 2008, Grüss et al. 2011). Although movement usually takes place in a heterogeneous landscape, and organisms are known to respond to a variety of landscape features (e.g., edges, habitat composition, and predation risk; Haynes and Cronin 2006, Nathan et al. 2008, Reeve and Cronin 2010, Abrams et al. 2012), the role of habitat-dependent movement (e.g., when the movement rate depends on the habitat; hereinafter referred to as differential movement) is not often considered in ecological models or management decisions.

The establishment of marine protected areas (MPAs) is a management tool used to increase biodiversity, population abundance, and/or fishing yield by reducing overfishing, habitat destruction, and by-catch. For example, MPAs can increase fishing yield by exporting adults and juveniles (via spillover) from the MPAs into fishing grounds (Abesamis

et al. 2006, Kellner et al. 2008). Movement of individuals directly influences spillover and thus the effectiveness of MPAs (Grüss et al. 2011). Most theoretical studies of MPAs, which have assumed random and homogeneous movement rates, have shown that increasing a species' overall mobility (e.g., average movement rate of non-larvae) decreases fish density in MPAs but increases fish density in the fishing grounds. As a result, the ratio of the density inside vs. outside the MPAs (hereinafter referred to as the "local effect") should decrease with increased mobility (see Gerber et al. 2003, Starr et al. 2004, Malvadkar and Hastings 2008). This decrease in the local effect results from increased mixing between the two habitats. However, empirical studies have failed to document the expected negative relationship between the local effect and mobility. Meta-analyses have either found no significant relationship (Micheli et al. 2004, Lester et al. 2009) or a possible positive relationship (Claudet et al. 2010).

To explain this apparent mismatch between theory and empirical results, some authors have suggested that fishing harvest, trophic interactions, and structure of fish assemblages would largely influence the densities inside and outside of MPAs, thus masking the expected negative effect of mobility on the local effect (Micheli et al. 2004, Palumbi 2004, Lester et al. 2009). While such explanations are valid, we suggest that the expectations from existing models might be misleading. Instead, we suggest that organisms might move differentially throughout an MPA network, rather than homogeneously as most existing models have assumed. One notable exception is Langebrake et al. (2012), who

proposed and theoretically evaluated two hypotheses to explain the mismatch between existing theory and data: (1) that organisms move at different rates in the MPA vs. in the fishing grounds (i.e., differential movement), and (2) that organisms actively bias their movement toward the MPA when they are at the reserve boundary, but otherwise move at similar rates in the two habitats (i.e., biased movement). They rejected the first hypothesis as a viable mechanism to explain the mismatch, but accepted the second. Here, we re-evaluate the differential movement hypothesis.

To test their differential movement hypothesis, Langebrake et al. (2012) assumed that fish and other harvested organisms move more in the fishing grounds where they are harvested and/or where the habitat has been degraded by fishing exploitation, and move less in MPAs where they are not harvested and/or where the habitat is in better condition. This habitat-specific movement pattern could result from ontogenetic shifts (Gerber et al. 2005), aggregative behavior (Eggleston and Parsons 2008), and/or behavioral responses to habitat structure (e.g., Tischendorf and Fahrig 2000, Baguette and Van Dyck 2007), mortality risk (Douglas-Hamilton et al. 2005, Eggleston and Parsons 2008, Januchowski-Hartley et al. 2012), or abiotic conditions (e.g., oil spill effects; see Fodrie et al. 2014). Higher mobility in the fishing grounds vs. the MPA could lead to net movement of individuals from the fishing grounds to the MPA, creating a spill-in pattern (in contrast to the classic spillover pattern; see Eggleston and Parsons [2008] for an empirical example of spill-in). This net movement could increase the local effect by increasing the density of the focal species in the MPA but decreasing its density in the fishing ground, thus potentially explaining the empirical results of Micheli et al. (2004), Lester et al. (2009), and Claudet et al. (2010). However, the above verbal argument, which motivated Langebrake et al.'s (2012) study, was not supported by their formal theoretical investigation.

Here, we propose that Langebrake et al. (2012) did not find a positive relationship between mobility and the local effect because of assumptions they made in analyzing their model. They developed a reaction–diffusion model that assumed that new organisms recruited via larval rain from outside the system, died at higher rates in the fishing grounds (due to harvesting), and moved at different rates inside vs. outside the MPA. They solved this model by constraining the density of the target organism to be continuous across the boundary between the MPA and the fishing grounds. However, fish density can abruptly change near boundaries (Chapman and Kramer 1999), and other theoretical studies have successfully modeled such discontinuities (Ovaskainen and Cornell 2003, Maciel and Lutscher 2013). The discontinuity at the boundary could influence population dynamics in different patches (see Maciel and Lutscher 2013), further influencing the equilibria and the local effect. We therefore hypothesized that the restrictive assumption that density was continuous across the MPA boundary may have been responsible for the failure of Langebrake et al. (2012) to produce flat or positive relationships between mobility and the local effect.

To address this conjecture and to re-evaluate the differential movement hypothesis, we studied the isolated and combined effects of differential movement and overall mobility

on several measures of MPA efficacy, but without assuming density continuity at the boundary. Because MPA size can influence the strength of animal movement as well as directly affect MPA efficacy (Pittman et al. 2014), we also considered the effect of the MPA size (relative to the fishing ground). We did this by building discrete spatial models: a two-patch box model in which one cell represents the MPA while the other represents the fishing ground, and a stepping-stone model in which fish moved between discrete cells along a linear shoreline. We first analytically solved the two-patch box model and then used numerical simulations to solve the multi-cell, stepping-stone model. In all cases, we examined how differential movement (i.e., the relative movement rate from one cell to another in the MPA vs. in the fishing grounds) and overall mobility (i.e., the overall magnitude of the movement rates) affected three indices reflecting the performance of MPAs: (1) the local effect (i.e., the density in the MPA relative to the density in the fishing grounds); (2) regional abundance (i.e., the combined abundance in both the MPA and the fishing grounds); and (3) fishing yield (assumed proportional to the product of the size of the fishing grounds and the density of the species in the fishing grounds). We also varied the relative sizes of the MPA and the fishing grounds by adjusting the proportion of cells in the landscape that were in the MPA or in the fishing grounds. To highlight the changes in abundances and/or densities resulting from the MPA, we rescaled the above three indices by their values before establishment of the MPA.

MODEL DEVELOPMENT

We built a discrete, one-dimensional spatial model (i.e., a stepping-stone model) in which fish moved between adjacent, discrete cells on a linear shoreline, along which MPAs and fishing grounds alternated periodically. The study region consisted of one of these repeating units, which was comprised of $S_M + S_F$ discrete and equal-sized cells: the MPA consisted of S_M cells and the fishing ground consisted of S_F cells (see Fig. 1). We used a circular representation of space by connecting the left side of the fishing ground with the right side of the MPA.

We developed three model structures depicting (1) an open system (with constant larval rain), (2) a closed system

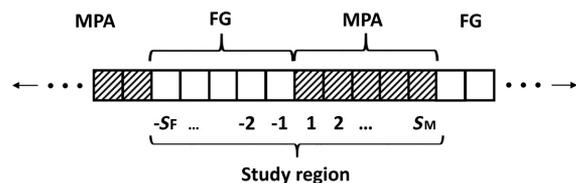


FIG. 1. A schematic of the linear study system, with marine protected areas (MPAs) and fishing grounds (FG) alternating along the coastline. Each cell (indicated by a square) has a length of 1 unit, and each MPA consists of S_M cells, while each fishing ground consists of S_F cells. Here, we show the case in which $S_M = S_F = 5$. Thus, the system we model, which represents a single MPA and fishing ground, is divided into $S_M + S_F$ cells with the boundary occurring between cell 1 (in the MPA) and cell -1 (in the FG). We wrap the MPA and fishing ground so that the S_M^{th} cell in the MPA connects to the $-S_F^{\text{th}}$ cell in the FG, thus creating a repeating linear system of MPAs and fishing grounds.

(with logistic growth in each cell), and (3) a semi-closed system (with logistic growth but larval redistribution among cells). For the open system, we assumed that the density of the focal species in each cell increased via constant larval recruitment (R); that is, we assumed that all reproduction came from outside the system because the MPA system was small relative to the dispersal ability of the organism. We then relaxed this assumption and explored a closed system by assuming logistic growth in a cell in which all larvae were retained locally (i.e., in the same cell as their parents). We then explored an intermediate version, for a semi-closed system, in which there was logistic growth within a cell but larvae were redistributed equally among all cells. Thus, these three models represent a gradient in the scale of the MPA–fishing-ground system relative to the scale of larval dispersal. We focus on the results of the open system (with constant larval rain) for its simplicity, but briefly summarize results for the two models with logistic growth (which are presented in more detail in the Appendix S1). In general, results regarding the effect of differential movement and mobility were similar for all three systems.

Organisms in all cells incurred the same intensity of natural mortality (μ_N), and organisms in the fishing grounds incurred additional mortality due to fishing (μ_F). We assumed that the mortality due to fishing (μ_F) was constant in each cell in the fishing ground and independent of the MPA size (as a special case, this can be achieved when there is no redistribution of fishing effort in response to the establishment of an MPA).

The dynamics within a cell were also affected by emigration to, and immigration from, the adjacent cells. We assumed that total emigration rate from each cell in the MPA was D_M , while it was D_F in the fishing ground, and that emigrants from a cell had the same chance of moving into either of the two adjacent cells (i.e., movement was not directed and there was no movement bias). Adopting the notation $N_{M,i}$ ($i = 1, 2, \dots, S_M$) for the density of the focal species in each MPA cell, where cells 1 and S_M are adjacent to the fishing grounds, and $N_{F,i}$ ($i = -S_F, \dots, -2, -1$) for the density in the fishing ground, with cells $-S_F$ and -1 adjacent to MPAs (see Fig. 1), these assertions led to the following model for the dynamics in the fishing grounds for the open system:

$$\frac{dN_{F,-S_F}}{dt} = R - (\mu_N + \mu_F)N_{F,-S_F} - D_F N_{F,-S_F} + \frac{D_F}{2} N_{F,-S_F+1} + \frac{D_M}{2} N_{M,S_M} \quad (1)$$

$$\frac{dN_{F,i}}{dt} = R - (\mu_N + \mu_F)N_{F,i} - D_F N_{F,i} + \frac{D_F}{2} (N_{F,i-1} + N_{F,i+1}) \quad (2)$$

for $i = -S_F + 1, \dots, -3, -2$

$$\frac{dN_{F,-1}}{dt} = R - (\mu_N + \mu_F)N_{F,-1} - D_F N_{F,-1} + \frac{D_F}{2} N_{F,-2} + \frac{D_M}{2} N_{M,1} \quad (3)$$

In the MPA (where there was no fishing mortality), we had

$$\frac{dN_{M,1}}{dt} = R - \mu_N N_{M,1} - D_M N_{M,1} + \frac{D_M}{2} N_{M,2} + \frac{D_F}{2} N_{F,-1} \quad (4)$$

$$\frac{dN_{M,i}}{dt} = R - \mu_N N_{M,i} - D_M N_{M,i} + \frac{D_M}{2} (N_{M,i-1} + N_{M,i+1}) \quad (5)$$

for $i = 2, 3, \dots, S_M - 1$

$$\frac{dN_{M,S_M}}{dt} = R - \mu_N N_{M,S_M} - D_M N_{M,S_M} + \frac{D_M}{2} N_{M,S_M-1} + \frac{D_F}{2} N_{F,-S_F} \quad (6)$$

When the size of the MPA and the fishing ground were equal (i.e., $S_M = S_F$), we sought an approach that would facilitate analytic solutions, so we simplified the model to have only two cells (i.e., $S_M = S_F = 1$). We refer to this model as a two-patch box model, which with constant larval rain becomes

$$\frac{dN_F}{dt} = R - (\mu_N + \mu_F)N_F - D_F N_F + D_M N_M \quad (7)$$

$$\frac{dN_M}{dt} = R - \mu_N N_M - D_M N_M + D_F N_F \quad (8)$$

Armed with insights from the box model, we then analyzed results of the stepping-stone model ($S_M + S_F > 2$). Although the stepping-stone model (Eqs. 1–6) can sometimes admit explicit analytic solutions, the resulting expressions are too cumbersome for subsequent analysis; hence we resorted to numerical simulations. We used a fixed landscape size (with $S_M + S_F = 10$), although simulations with larger landscapes demonstrated that the qualitative patterns were unaffected by the number of cells in the study system. We first simulated the results prior to establishment of the MPA (i.e., when all cells were fished) to provide a baseline from which to evaluate effects of protection. We then simulated the responses after establishment of the MPA network to study the combined effects of differential movement, overall mobility, and the relative size of the MPA ($S_M/(S_M + S_F)$) on the average density within each habitat and on the spatial pattern in density across the entire MPA–fishing-ground system.

For analyses of the box model and simulations of the stepping-stone model, we focused on the local effect, regional abundance, and fishing yield. For ease of interpretation of figures, we rescaled all responses relative to their value before establishing the MPA. Note that by definition the local effect was equal to 1 before the MPA was established, so for this response variable rescaling had no effect.

After exploring the behavior of the open system (with constant larval rain), we then briefly explored results for the closed and semi-closed systems. For the closed system (with logistic growth, but without larval redistribution), we simply replaced the recruitment term, R , in Eqs. 1–6 with a logistic term representing gains via recruitment and losses via density-dependent mortality, $rN_{j,i} - rN_{j,i}^2/K$, where r is per capita growth rate, K is the carrying capacity of any cell (we assumed r and K were the same in the MPA and fishing grounds, and $N_{j,i}$ is the density in cell i in habitat j). For the semi-closed system, we assumed that larvae were well mixed and redistributed uniformly among all cells in the system,

rather than being retained locally. Thus, for the semi-closed system, we replaced the recruitment term in the logistic (i.e., rN) with $\frac{1}{S_M+S_F} \left(r_F \sum_{i=-S_F}^{-1} N_{F,i} + r_M \sum_{i=1}^{S_M} N_{M,i} \right)$. For the closed system, we analytically solved the two-patch box model and then simulated results for the stepping-stone model. However, the semi-closed system was more complex, so we restricted our analyses to simulations of the two-patch box model as well as the stepping-stone model.

RESULTS

The open system (constant larval rain)

The two-patch box model.—This model (Eqs. 7 and 8) has the following analytical solutions for the densities of organisms in the MPA and the fishing ground:

$$N_F^* = \frac{R(\mu_N + 2D_M)}{(\mu_N + \mu_F + D_F)\mu_N + (\mu_N + \mu_F)D_M} \tag{9}$$

$$N_M^* = \frac{R(\mu_N + \mu_F + 2D_F)}{(\mu_N + \mu_F + D_F)\mu_N + (\mu_N + \mu_F)D_M} \tag{10}$$

By setting $\frac{D_F}{D_M} = \beta$, the strength of differential movement, the above solutions can be rearranged as

$$N_F^* = \frac{R(\mu_N + 2D_M)}{(\mu_N + \mu_F + \beta D_M)\mu_N + (\mu_N + \mu_F)D_M} \tag{11}$$

$$N_M^* = \frac{R(\mu_N + \mu_F + 2\beta D_M)}{(\mu_N + \mu_F + \beta D_M)\mu_N + (\mu_N + \mu_F)D_M} \tag{12}$$

From Eqs. 11 and 12, we derive the influence of differential movement on the densities of organisms in each cell by differentiating Eqs. 11 and 12 with respect to β

$$\frac{d(N_M^*)}{d\beta} = \frac{RD_M(\mu_N + \mu_F)(\mu_N + 2D_M)}{[(\mu_N + \mu_F + \beta D_M)\mu_N + (\mu_N + \mu_F)D_M]^2} > 0 \tag{13}$$

$$\frac{d(N_F^*)}{d\beta} = \frac{-R\mu_N D_M(\mu_N + 2D_M)}{[(\mu_N + \mu_F + \beta D_M)\mu_N + (\mu_N + \mu_F)D_M]^2} < 0 \tag{14}$$

Therefore, in the system with constant larval rain, increasing differential movement always increases the density in the MPA and always decreases the density in the fishing grounds. From Eqs. 11 and 12, we can also solve for the local effect

$$\frac{N_M^*}{N_F^*} = \frac{\mu_N + \mu_F + 2\beta D_M}{\mu_N + 2D_M}$$

the regional abundance

$$N_M^* + N_F^* = \frac{R[2\mu_N + \mu_F + 2D_M(1 + \beta)]}{(\mu_N + \mu_F + \beta D_M)\mu_N + (\mu_N + \mu_F)D_M}$$

and the fishing yield, which is equal to N_F^* (Eq. 11) times the mortality due to fishing (μ_F) and the size of the fishing grounds (S_F): that is, $\mu_F S_F N_F^*$.

These solutions can be differentiated with respect to β , to determine how the solutions change as differential movement, β , increases

$$\frac{d\left(\frac{N_M^*}{N_F^*}\right)}{d\beta} = \frac{2D_M}{\mu_N + 2D_M} > 0 \tag{15}$$

$$\frac{d(N_M^* + N_F^*)}{d\beta} = \frac{RD_M \mu_F (\mu_N + 2D_M)}{[(\mu_N + \mu_F + \beta D_M)\mu_N + (\mu_N + \mu_F)D_M]^2} > 0 \tag{16}$$

$$\frac{d(\mu_F S_F N_F^*)}{d\beta} = \frac{-\mu_F S_F R D_M \mu_N (\mu_N + 2D_M)}{[(\mu_N + \mu_F + \beta D_M)\mu_N + (\mu_N + \mu_F)D_M]^2} < 0 \tag{17}$$

Thus, increasing differential movement always increases the local effect ($\frac{N_M^*}{N_F^*}$; Eq. 15) and the regional abundance ($N_M^* + N_F^*$; Eq. 16), but decreases fishing yield ($\mu_F S_F N_F^*$; Eq. 17; Fig. 2).

We then evaluated the effect of overall mobility on the local effect, regional abundance, and fishing yield, for a given level of differential movement (assuming $\beta \geq 1$: that is, movement rate in the fishing grounds was always greater than or equal to movement rate in the MPA). For a given strength of differential movement, changing D_M induces an equivalent relative change in D_F , so we use D_M to indicate the overall mobility. The effect of overall mobility on the three measures of MPA efficacy is

$$\frac{d\left(\frac{N_M^*}{N_F^*}\right)}{dD_M} = \frac{2\mu_N(\beta - 1) - 2\mu_F}{(\mu_N + 2D_M)^2} \tag{18}$$

$$\frac{d(N_M^* + N_F^*)}{dD_M} = \frac{R\mu_F[(\beta - 1)\mu_N - \mu_F]}{[(\mu_N + \mu_F + \beta D_M)\mu_N + (\mu_N + \mu_F)D_M]^2} \tag{19}$$

$$\frac{d(\mu_F S_F N_F^*)}{dD_M} = \frac{\mu_F S_F R \mu_N [(1 - \beta)\mu_N + \mu_F]}{[(\mu_N + \mu_F + \beta D_M)\mu_N + (\mu_N + \mu_F)D_M]^2} \tag{20}$$

Eqs. 18–20 demonstrate that the correlations between mobility and the local effect (Eq. 18), regional abundance (Eq. 19), and fishing yield (Eq. 20) depend on the strength of differential movement (β). In the absence of differential movement ($\beta = 1$), increasing mobility decreases the local effect

$\left(\frac{d\left(\frac{N_M^*}{N_F^*}\right)}{dD_M} < 0\right)$ and regional abundance $\left(\frac{d(N_M^* + N_F^*)}{dD_M} < 0\right)$, but

increases fishing yield $\left(\frac{d(\mu_F S_F N_F^*)}{dD_M} > 0\right)$; see the relative loca-

tions of the three lines at $\beta = 1$ in Fig. 2 and the solid line in Fig. 3. These results reiterate those of past theoretical studies (e.g., Gerber et al. 2003, Starr et al. 2004, Malvadkar and Hastings 2008). However, in the presence of differential movement ($\beta > 1$), the sign of these derivatives (Eqs. 18 and 20) depends on the relative mortality rates in the fishing grounds ($\mu_N + \mu_F$) vs. the MPA (μ_N). When the differential movement parameter is smaller than the relative mortality rates (i.e., $1 < \beta < (\mu_N + \mu_F)/\mu_N$), the qualitative patterns are

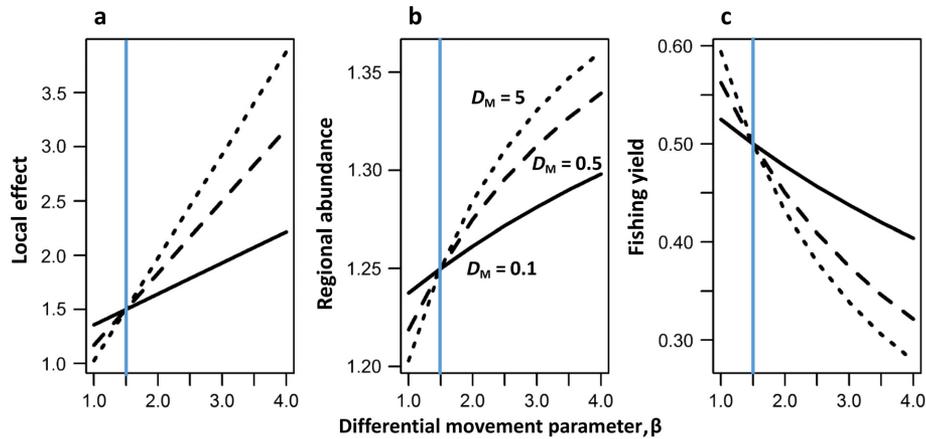


FIG. 2. The effect of differential movement ($\beta = D_F/D_M$; where β is differential movement, D_M is total emigration rate from each cell in the MPA, and D_F is emigration rate in the fishing ground) on (a) the local effect (density ratio of the MPA and fishing grounds), (b) regional abundance, and (c) fishing yield at equilibrium under three levels of mobility ($D_M = 0.1$ [solid line], 0.5 [dashed], and 5 [dotted]) in the two-patch box model for the open system (i.e., with larval rain). The blue line indicates the value of the differential movement parameter at which the local effect shifts from decreasing to increasing with an increase in mobility ($\beta = (\mu_N + \mu_F)/\mu_N = 1.5$; where μ_N is the natural mortality rate and μ_F is the additional mortality in the fishing grounds). Other parameters: larval recruitment $R = 2$, $\mu_N = 0.5$, $\mu_F = 0.25$. All results are rescaled relative to their values before establishing the MPA.

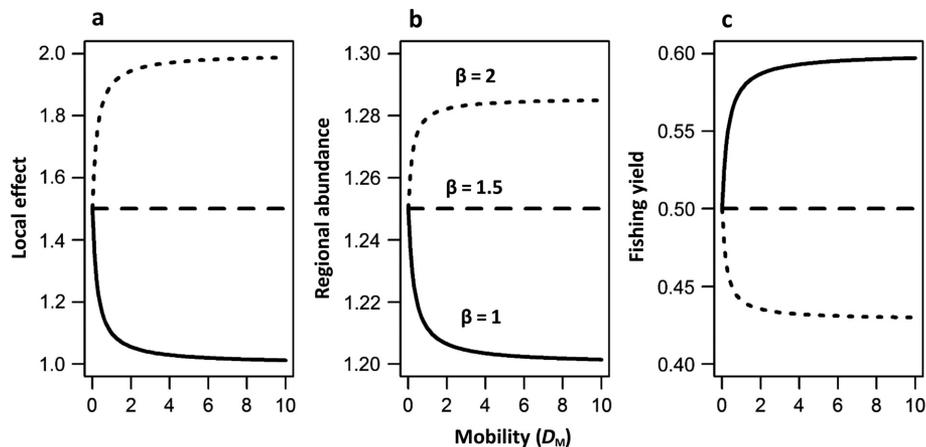


FIG. 3. The effect of mobility (D_M) on (a) the local effect (density ratio of MPA and fishing grounds), (b) regional abundance, and (c) fishing yield under three levels of differential movement ($\beta = 1$ [solid line], 1.5 [dashed], and 2 [dotted line]), corresponding to values smaller than, equal to, and larger than $(\mu_N + \mu_F)/\mu_N$, in the two-patch box model for the open system (i.e., with larval rain). Other parameters are $R = 2$, $\mu_N = 0.5$, $\mu_F = 0.25$. All results are rescaled relative to their values before establishing the MPA.

identical to the results when there is no differential movement (i.e., when $\beta = 1$). When the differential movement parameter is equal to the relative mortality rates in the two patches (i.e., $\beta = (\mu_N + \mu_F)/\mu_N$, represented by the blue line in Fig. 2), the spatial patterns are independent of the overall movement rate (note the crossing of the three lines in Fig. 2 and the horizontal dashed line in Fig. 3). However, when the differential movement parameter exceeds the relative mortality rates (i.e., $\beta > (\mu_N + \mu_F)/\mu_N$), increasing mobility increases the local effect, and increases regional abundance, but decreases fishing yield (see the relative locations of the three lines on the right of the blue line in Fig. 2 and the dotted line in Fig. 3). Thus, if differential movement is sufficiently strong (i.e., if the movement rates in the two habitats are at least as dissimilar as their respective mortality rates), it can explain the discrepancy between previous theoretical results (which assumed equal movement rates) and the

empirical studies that either found no significant relationship (Micheli et al. 2004, Lester et al. 2009) or a possible positive relationship (Claudet et al. 2010), between the local effect and mobility.

The stepping-stone model.—As differential movement increased, the local effect also increased (Fig. 4 and Appendix S1: Fig. S5). Although regional abundance increased and fishing yield decreased, these responses were negligible (Fig. 4 and Appendix S1: Fig. S5). Overall, these qualitative results are consistent with our analyses of the two-patch box model (Eqs. 15–17).

Increasing the relative MPA size led to a marked increase in regional abundance and decrease in fishing yield (Fig. 4b, c). However, the local effect showed a more complex pattern with respect to relative MPA size. The local effect increased more as differential movement increased when the MPA was

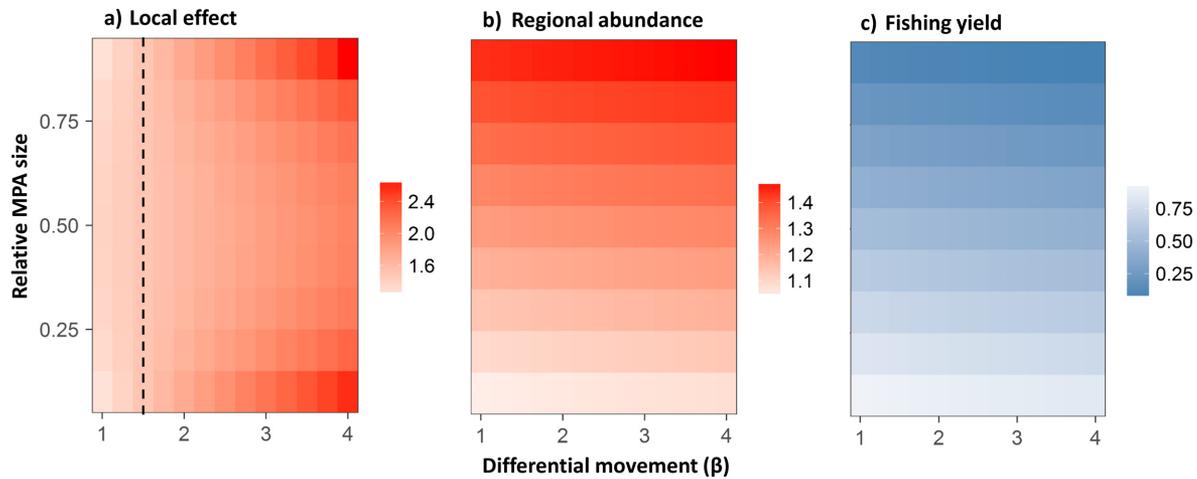


FIG. 4. The effect of the relative MPA size ($S_M/(S_M + S_F)$; where S_M is the size of the MPA and S_F is the size of the fishing ground) and the differential movement parameter (β) on (a) the local effect (density ratio of MPA and fishing grounds), (b) regional abundance, and (c) fishing yield in the stepping-stone model for the open system (i.e., with larval rain). All results are rescaled relative to their values before establishing the MPA. Shades of red color (values >1) indicate an increase relative to conditions before establishment of the MPA, whereas blue indicates a decrease and white indicates no change (i.e., values equal to 1). The dashed line in panel a indicates the differential movement parameter at which the local effect is independent of the relative size of the MPA ($\beta = 1.5 = (\mu_N + \mu_F)/\mu_N$). Other parameters: $R = 2$, $\mu_N = 0.5$, $\mu_F = 0.25$, $S_M + S_F = 10$, and $D_M = 0.5$.

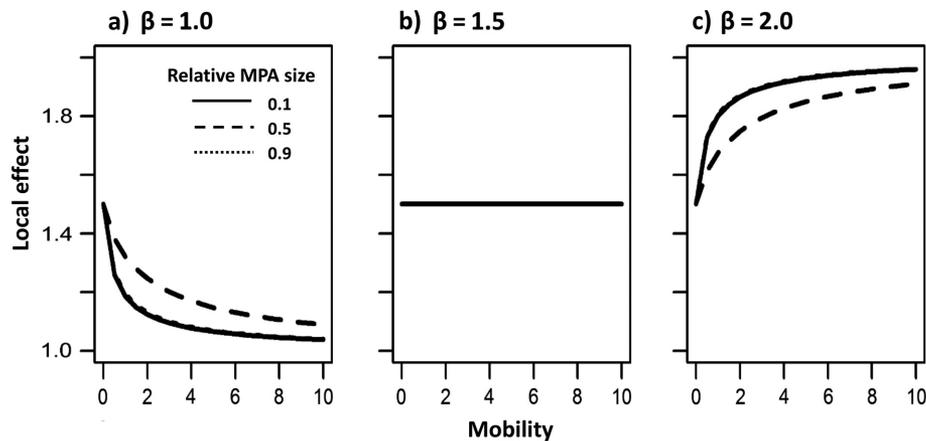


FIG. 5. The effect of mobility on the local effect (density ratio of MPA and fishing grounds) for the stepping-stone model of the open system (i.e., with larval rain) evaluated for three relative sizes of the MPA ($S_M/(S_M + S_F) = 0.1, 0.5$, and 0.9) and three levels of differential movement: (a) $\beta = 1.0$, (b) $\beta = 1.5$, and (c) $\beta = 2.0$, corresponding to values smaller than, equal to, and larger than $(\mu_N + \mu_F)/\mu_N$. Note that the solid and dotted lines in panels a and c overlap, as do all three lines in panel b. Other parameters: $R = 2$, $\mu_N = 0.5$, $\mu_F = 0.25$, and $S_M + S_F = 10$. All results are rescaled relative to their values before establishing the MPA.

either relatively large or relatively small; the effect of increasing differential movement was smallest at intermediate MPA sizes (Fig. 4a). When differential movement was equal to the critical value (i.e., $\beta = (\mu_N + \mu_F)/\mu_N$), the local effect did not change with the relative MPA size (see the dashed line in Fig. 4a). However, when differential movement was smaller than this value ($1 \leq \beta < (\mu_N + \mu_F)/\mu_N$; on the left side of the dashed line in Fig. 4a), the local effect initially increased (as the relative MPA size increased from 0 to 0.5), but then decreased (as the relative MPA size increased from 0.5 to 1.0), although the small change is hard to discern in Fig. 4a. In contrast, when differential movement was larger than this critical value ($\beta > (\mu_N + \mu_F)/\mu_N$), the local effect first decreased then increased as the relative size of the MPA increased.

The magnitude of differential movement determined the relationship between mobility and the local effect: when $\beta < (\mu_N + \mu_F)/\mu_N$, the spillover pattern existed, leading to a negative relationship between mobility and the local effect (when Eq. 18 < 0 ; Fig. 5a); when $\beta = (\mu_N + \mu_F)/\mu_N$, there was a constant local effect (Eq. 18 = 0; Fig. 5b); and when $\beta > (\mu_N + \mu_F)/\mu_N$, the spill-in pattern occurred, leading to a positive relationship between mobility and the local effect (Fig. 5c). These qualitative effects on the local effect held across MPA sizes (Fig. 5).

We also explored the spatial patterns that arose within a habitat and across the MPA-fishing ground boundary to gain insights about differential movement and its relationship to past theoretical results. We simulated the density in each cell across the entire study region under three levels of

differential movement: that is, when β was smaller than, equal to, or larger than the relative mortality rates $(\mu_N + \mu_F)/\mu_N$. When $\beta = (\mu_N + \mu_F)/\mu_N$, densities within each habitat were homogeneous: that is, there was no spatial heterogeneity within the MPA or the fishing grounds, but there was a sharp density difference at the boundary between the MPA and fishing grounds (Fig. 6b). However, when $\beta \neq (\mu_N + \mu_F)/\mu_N$, densities were heterogeneous within habitats, with density in a cell depending on the cell's distance from the MPA boundary. Importantly, the density difference across the boundary of the MPA shifted from smooth (when $\beta < (\mu_N + \mu_F)/\mu_N$; Fig. 6a) to abrupt (when $\beta \geq (\mu_N + \mu_F)/\mu_N$; Fig. 6b, c). Specifically, when differential movement was small (Fig. 6a: $\beta < (\mu_N + \mu_F)/\mu_N$), densities in the fishing grounds were greatest near the MPA boundary, but lowest in the center. In contrast, densities in the MPA were lowest at the boundary and greatest at the center. These smooth transitions are consistent with the spillover pattern classically described in models of MPA systems (see Gerber et al. 2003, Starr et al. 2004, Malvadkar and Hastings 2008). However, when differential movement was large (Fig. 6c: $\beta > (\mu_N + \mu_F)/\mu_N$), the pattern reversed. Densities in the fishing grounds were depressed near the MPA border and greatest at the center of the fishing grounds. Densities in the MPA were greatest near the boundary and depressed in the center of the MPA. These patterns are indicative of spill-in dynamics. These qualitative patterns were observed across all relative MPA sizes (see Appendix S1: Fig. S1).

The closed system (logistic growth without larval redistribution)

The two-patch box model.—Changing the form of the recruitment term from larval rain to logistic growth without larval redistribution (Appendix S1: Eqs. S1–S6) had relatively little

effect on the qualitative responses regarding the local effect and further highlighted the important role played by differential movement. For example, the relationship between mobility and the local effect depended on the magnitude of differential movement; however, the transition from a negative to a positive relationship occurred when $\beta = \frac{r-\mu_N}{r-\mu_N-\mu_F}$ instead of $\beta = (\mu_N + \mu_F)/\mu_N$. In other words, when $1 \leq \beta < \frac{r-\mu_N}{r-\mu_N-\mu_F}$, the typical spillover pattern occurred (Appendix S1: Eq. S19); and when $\beta > \frac{r-\mu_N}{r-\mu_N-\mu_F}$, the spill-in pattern occurred (Appendix S1: Eq. S20): see Appendix S1: Fig. S4d).

This critical value of differential movement ($\beta = \frac{r-\mu_N}{r-\mu_N-\mu_F}$; in this case, $\beta = 2$) also defined the conditions under which the regional abundance and fishing yield did not change with increased mobility (Appendix S1: Fig. S4e, f). In comparison with the open system, the qualitative pattern of change in regional abundance was a bit more complex: with an increase in β , the regional abundance decreased (compare the three lines in Fig. S4e), whereas in the open system, the regional abundance increased (Appendix S1: Fig. S4b). In addition, the relationship between regional abundance and mobility was not always monotonic: for example, when $\beta < \frac{r-\mu_N}{r-\mu_N-\mu_F}$ (the solid black line in Appendix S1: Fig. S4e), regional abundance first increased then decreased with the increase of mobility (see also Appendix S1: Eq. S29 and associated text in the Appendix S1). Patterns of change in fishing yield were consistent with results from the open system.

The stepping-stone model.—Extension of the two-patch model to the stepping-stone model further demonstrated the role of differential movement and showed that spatial patterns were not qualitatively affected by changing the recruitment from constant larval rain to local recruitment (i.e., comparing the open vs. closed system). When differential movement was small or absent (when $\beta < \frac{r-\mu_N}{r-\mu_N-\mu_F}$), densities

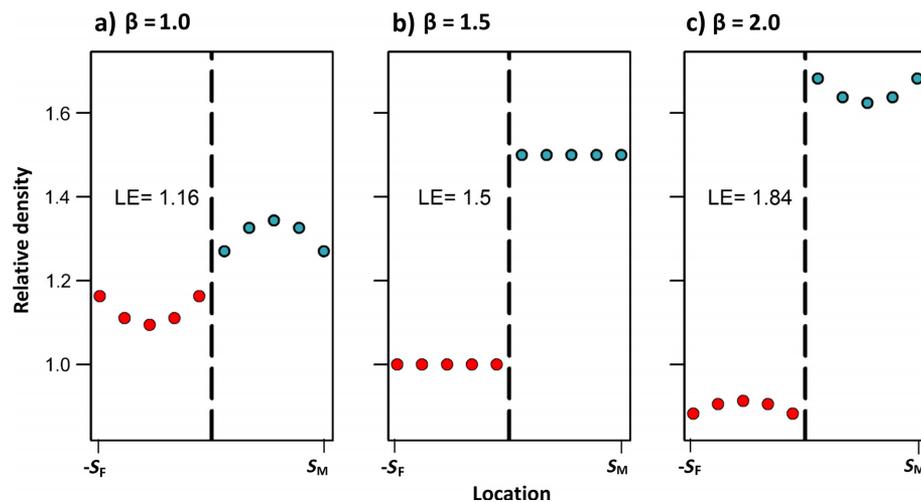


FIG. 6. Relative local densities (rescaled relative to their values before the MPA establishment) in the MPA (in blue and to the right of the vertical line) and fishing grounds (in red and to the left of the vertical line) for the stepping-stone model of the open system (i.e., with constant larval rain) under three levels of differential movement ($\beta = 1.0, 1.5,$ and 2.0) when the MPA and fishing grounds are equal in size ($S_M/(S_M + S_F) = 0.5$; see Appendix S1: Fig. S1 for results when the MPA and fishing grounds are of different sizes). The three values for the differential movement parameter correspond to values smaller than, equal to, and larger than $(\mu_N + \mu_F)/\mu_N$. Note that for $\beta = 1.0$, the density changes smoothly across space, but for $\beta \geq 1.5$, the density changes abruptly across the MPA boundary. Also given on each panel is the local effect (LE: the density ratio of the MPA and fishing grounds). Other parameters: $R = 2$, $\mu_N = 0.5$, $\mu_F = 0.25$, and $S_M + S_F = 10$.

changed relatively smoothly within habitats and across the MPA boundary (Appendix S1: Fig. S2a, d, g). However, when $\beta = \frac{r-\mu_N}{r-\mu_N-\mu_F}$, densities within habitats were homogeneous, and the local effect was independent of the relative MPA size (Appendix S1: Fig. S2b, e, h). When differential movement was even larger ($\beta > \frac{r-\mu_N}{r-\mu_N-\mu_F}$), densities were heterogeneous within habitats and changed abruptly across the MPA boundary (Appendix S1: Fig. S2c, f, i). The regional abundance and fishing yield decreased with differential movement, consistent with what we observed in the two-patch box model (compare Appendix S1: Fig. S4e, f and the middle and right-hand columns of Appendix S1: Fig. S6).

The semi-closed system (logistic growth with larval redistribution)

The two-patch box model.—Analytic solutions to the model for the semi-closed system (even with only two patches) were more difficult to obtain than for the other two systems; therefore, we focused exclusively on simulation. As seen with the other two systems, the effect of mobility on the local effect depended on the degree of differential movement. There was a critical value of β that distinguished the local effect increasing vs. decreasing with mobility (Appendix S1: Fig. S4). Based on the parameter values used in our simulations, this critical value occurred at ~ 1.2 , which was less than the critical value obtained analytically for the closed system (i.e., $\frac{r-\mu_N}{r-\mu_N-\mu_F}$).

Fishing yield exhibited a similar pattern as in the open system; for example, fishing yield decreased as differential movement increased, and increasing mobility caused fishing yield to increase when differential movement was greater than the critical value but decrease when differential movement was less than the critical value (Appendix S1: Fig. S4i). Regional abundance showed a more complex pattern with differential movement that was a composite of the patterns observed for the open and the closed systems. When differential movement was relatively small (smaller than the critical value; see the solid and dashed lines in Appendix S1: Fig. S4 h), regional abundance increased with differential movement, as observed in the open system (Appendix S1: Fig. S4b). When differential movement was relatively large (see the dotted and the dash-dotted lines in Appendix S1: Fig. S4 h), regional abundance decreased with differential movement, as observed in the closed system (Appendix S1: Fig. S4e).

The stepping-stone model.—The density pattern across the whole study area resulting from differential movement exhibited similar qualitative patterns as observed in the closed and open systems (Appendix S1: Fig. S3): for example, at the critical value of differential movement, there was constant density within the MPA (or fishing grounds, Appendix S1: Fig. S3b, f, j), but above or below this critical value, we observed spill-in (Appendix S1: Fig. S3a, e, i) or spill-out (Appendix S1: Fig. S3c, d, g, h, k, l), respectively. Additional results for regional abundance and fishing yield were more complex than for the open system and depended on both relative MPA sizes and fishing mortalities (Appendix S1: Fig. S7).

DISCUSSION

This study used both analytical and numerical methods to determine how differential movement, overall mobility, and relative size of the MPA altered the local effect (density ratio of MPA and fishing ground), regional abundance, and fishing yield of a population that is partially protected by a marine reserve. Our results show that the degree of differential movement alters the local effect, regional abundance, fishing yield, and spatial patterns within and across habitats. These results were robust and qualitatively unaffected by altering our assumptions about the scale of larval dispersal and density dependence. In all cases, there was a critical value of differential movement that distinguished between spill-in and spill-out patterns. When differential movement was smaller than the critical value, we observed a spill-out pattern. When differential movement was larger than the critical value, we observed spill-in patterns.

Previous models (e.g., Gerber et al. 2003, Malvadkar and Hastings 2008) assumed movement rates were homogeneous across the landscape (i.e., $\beta = 1$), and therefore have generated a body of knowledge focused on spill-out phenomena. For example, these classic models predict that the local effect declines with increased mobility: that is, increased mixing between the fishing grounds and MPA homogenizes the system. In contrast, our results revealed that if organisms move at sufficiently different rates inside vs. outside of MPAs, increasing overall mobility can enhance the local effect (see Figs. 2, 3, 5, and Appendix S1: Fig. S4). This means that groups of species with similar movement patterns inside and outside an MPA could show negative relationships between mobility and the local effect, while taxa with more disparate rates of movement in the two habitats could show no relationship, and taxa with even larger differences in their movement rates could show a positive relationship between mobility and the local effect. Because meta-analyses have found either no average effect (Micheli et al. 2004, Lester et al. 2009), or suggested a possible positive effect of mobility on the local effect (Claudet et al. 2010), we suggest that differential movement should be considered as one possible hypothesis to explain the discrepancy between empirical data and previous theoretical investigations of mobility.

This conclusion contrasts with that of Langebrake et al. (2012). Our study demonstrates that differential movement can produce an abrupt change in density near the boundary between the MPA and the fishing grounds (see Fig. 6 and Appendix S1: Figs. S1–S3; see also Ovaskainen and Cornell 2003, Maciel and Lutscher 2013). This pattern suggests that Langebrake et al.'s (2012) differential movement model, in which they imposed continuity in a reaction-diffusion model, may have provided a misleading evaluation of the effects of differential movement on a population's response to protection.

The effect of differential movement on the local effect (as well as regional abundance and fishing yield) is explicitly linked to the local demographic rates (Fig. 5 and Appendix S1: Fig. S4). The establishment of an MPA creates a higher density of fish in the MPA relative to the fishing ground due to reduced mortality in the MPA. Assuming equal movement rates in the two habitats, this difference in density provides a net movement from the MPA to the

fishing ground (i.e., spillover), which tends to reduce the density difference between the two habitats. At larger mobility rates, the density disparity is homogenized further and the local effect declines. However, when differential movement occurs, and is sufficiently large to counterbalance the effect of differential recruitment and mortality inside vs. outside the MPA, it can swamp the effect of the density difference, giving rise to a spill-in pattern. Under this spill-in pattern, increased mobility exacerbates the density difference between the habitats: that is, the density in the MPA increases, the density in the fishing grounds decreases, and the local effect increases. When the differential movement just offsets the spillover potential (i.e., β equals the critical value), there is no net movement between the MPA and the fishing grounds. Thus, the density in each habitat is only determined by habitat-specific demographic rates (e.g., see Appendix S1: Eqs S11 and S12) and the local effect does not depend on the relative size of the MPA or the organism's mobility: Figs. 2a, 3, 4a, 5b, and Appendix S1: S1–S4).

Theoretical models (Ovaskainen and Cornell 2003, Langebrake et al. 2012, Maciel and Lutscher 2013, Brochier et al. 2015) have demonstrated that a movement bias at the MPA boundary toward the MPA can produce spatial patterns similar to those seen in our model of differential movement. Both behavioral processes (movement bias and differential movement) can extend the relative residence time of individuals in MPAs and further increase the local effect. Biologically speaking, movement bias is thought to be an adaptation to sharp patch edges, environmental gradients, and/or highly dynamic landscapes (Fagan et al. 2017). It requires that organisms be able to perceive and orient toward different environmental conditions over spatial scales relevant to the level of contrast of the environmental gradients or to the sharpness of patch edges (Benhamou and Bovet 1989, Nathan et al. 2008, Fagan et al. 2017). Many animals bias their movement, but there is high variation in their ability to do so or in the environmental gradient (or grain) to which they can react (e.g., Ries and Debinski 2001, Fagan et al. 2017).

In contrast, differential movement is advantageous for foraging individuals in coarse-grained, highly heterogeneous and patchy environments (Benhamou 1992). Differential movement requires that individuals perceive local conditions and modify their movement speed and/or sinuosity (e.g., turning angles) to intensify their use of space in profitable (or safe) areas, and thus differential movement can be used even if patch boundaries are non-perceptible (Benhamou 1992). Note that in the present study, where we used a one-dimensional and discrete representation of space, the movement rates between cells represent a higher scale consequence of within-cell movements: as individuals modify their movement speed and/or sinuosity within cells in response to local conditions, this modifies the between-cell movement rates. Both movement bias and differential movement are very common in nature, and are likely to be driven by differences in habitat quality (Grüss et al. 2011, Dixon and Hay 2012) or by fishing activities (e.g., boat noise; see Sarà et al. 2007, Simpson et al. 2016), and probably both play some role in MPA systems. This role will depend on the extent of the environmental differences inside vs. outside the MPA, the sharpness of the MPA edges, and on the fish's

ability to perceive them, and should be empirically investigated in the future.

To discriminate between the roles of differential movement and movement bias, we should ideally compare movement rates inside vs. outside of MPAs and patterns of movement at the edges of MPAs. Unfortunately, we know of no relevant field measurements in the context of MPA systems. Although many studies have quantified movement in MPAs (Pittman et al. 2014), none have compared movement rates in the MPA with movement rates in the fishing grounds nor have any quantified movement at the MPA boundaries (although the data on home range size by Parsons et al. (2010) are supportive of the differential movement hypothesis; see also a terrestrial example by Douglas-Hamilton et al. (2005), which showed that elephants move more outside of protected areas).

Importantly, differential movement (or movement bias) could lead to a local effect even in the absence of differential mortality. If fishing mortality is absent, the local effect with differential movement (in the box model for the open system) becomes: $\frac{N_M^*}{N_F^*} = \frac{\mu_N + 2\beta D_M}{\mu_N + 2D_M}$. In the absence of differential movement ($\beta = 1$), there is no difference in density between the MPA and fishing grounds; however, for $\beta > 1$, a local effect (with an abrupt change across the boundary) emerges even without fishing-induced mortality (i.e., $N_M^* > N_F^*$; inferred from $\frac{N_M^*}{N_F^*} = \frac{\mu_N + 2\beta D_M}{\mu_N + 2D_M}$ and $\beta > 1$). Therefore, differential movement can inflate the local effect, potentially giving a perception of a demographic benefit, when in fact, it primarily reflects a behavioral response to human activities.

The field study by Eggleston and Parsons (2008) bears directly on this point. They compared the change in density of lobsters inside vs. outside of MPAs in the Florida Keys over an intense, three-day, recreational fishing window. As a result of the short duration of the study, there was no input of lobsters to the system during the study, only extraction and potential redistribution. As expected, lobster density outside the MPAs declined. However, lobster density inside the MPAs *increased*: there was a net movement of lobster from the fishing grounds into the MPAs presumably because they moved more in the fishing grounds and moved less in the MPAs (e.g., due to differences in fishing-induced disturbance), and/or lobsters near the MPA boundary biased their movement toward the MPA. As a result, the behavioral response of the lobsters magnified the local effect that would have been produced via differences in mortality alone.

We have emphasized the situation in which animal movement is potentially greater in the fishing grounds (i.e., $\beta > 1$). However, some species reduce their activity levels in the face of additional risk (e.g., freezing behavior; Takahashi et al. 2005, Werner and Peacor 2003), and some species may encounter greater densities of their predators in the MPA. These types of non-consumptive effects (see Peacor 2002, Preisser et al. 2009) from fishing activity could thus either enhance (if $\beta > 1$) or reduce (if $\beta < 1$) the movement of animals between the fishing grounds and the MPA. Future studies in marine conservation and fisheries management, especially with respect to MPAs, should consider these direct and indirect influences of fishing (i.e., differential mortality as well as movement) on spatial patterns, population dynamics, and sustainability (e.g., Walters and Juanes 1993, Pine et al. 2009). Distinguishing effects of movement and

demography is especially crucial because movement could lead to misinterpretation about the efficacy of management strategies and their effects on species conservation.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2477/supinfo>

DATA AVAILABILITY

The R code supporting the results is available from Zenodo: <https://doi.org/10.5281/zenodo.1402783>

APPENDIX

Habitat-dependent movement rate can determine the efficacy of marine protected areas.

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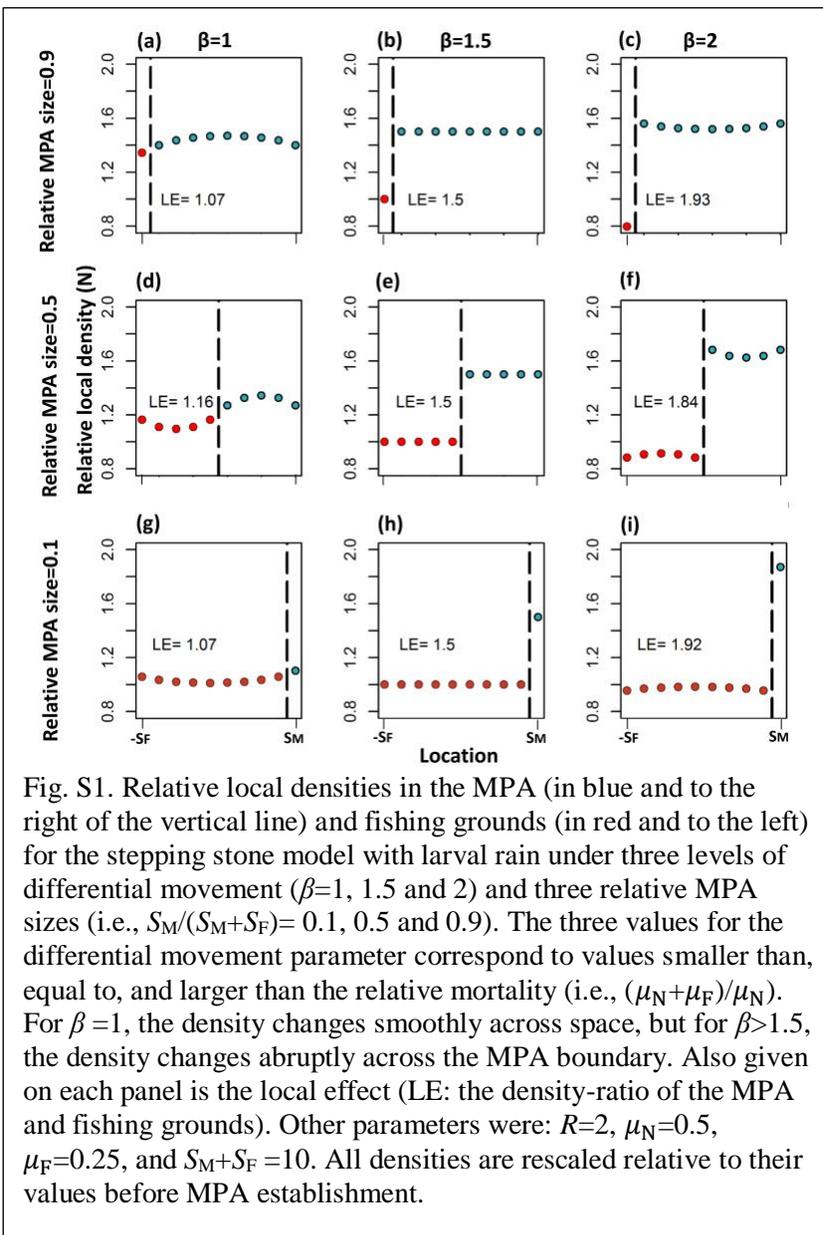


Fig. S1. Relative local densities in the MPA (in blue and to the right of the vertical line) and fishing grounds (in red and to the left) for the stepping stone model with larval rain under three levels of differential movement ($\beta=1, 1.5$ and 2) and three relative MPA sizes (i.e., $S_M/(S_M+S_F)=0.1, 0.5$ and 0.9). The three values for the differential movement parameter correspond to values smaller than, equal to, and larger than the relative mortality (i.e., $(\mu_N+\mu_F)/\mu_N$). For $\beta=1$, the density changes smoothly across space, but for $\beta>1.5$, the density changes abruptly across the MPA boundary. Also given on each panel is the local effect (LE: the density-ratio of the MPA and fishing grounds). Other parameters were: $R=2, \mu_N=0.5, \mu_F=0.25$, and $S_M+S_F=10$. All densities are rescaled relative to their values before MPA establishment.

SECTION 1: THE STEPPING-STONE MODEL FOR THE OPEN SYSTEM: THE EFFECTS OF MPA SIZE

In the main text, we provide results for the stepping stone model for the open system (i.e., with larval rain), when the MPA and fishing grounds are of equal size ($S_M/(S_M+S_F) = 0.5$). Here (Fig. S1), we also provide results when $S_M/(S_M+S_F) = 0.1$ and 0.9 . The qualitative patterns are the same across all three MPA sizes: for equal rates of movement in

the two habitats (i.e., $\beta = 1$), there is a gradient in density within each habitat (e.g., densities in the MPA are greatest near the border with the fishing ground) and densities change smoothly across the MPA-fishing ground border. However, when the differential movement parameter equals the relative mortality rate (i.e., $\beta = (\mu_N + \mu_F)/\mu_N$, which in this case is 1.5), then densities are constant within each habitat and there is an abrupt transition across the border between the MPA and fishing grounds (Fig. S1, middle column). Under more extreme values of differential movement (i.e., $\beta > (\mu_N + \mu_F)/\mu_N$), there is again a density gradient within each habitat although the pattern is opposite that is seen when $\beta = 1$: e.g., the density in the MPA is greatest in the middle of the MPA and lowest in the middle of the fishing grounds (Fig. S1, right hand column).

SECTION 2: CLOSED SYSTEM (LOGISTIC GROWTH WITHOUT LARVAL REDISTRIBUTION)

2.1 The basic model

Replacing constant larval rain (R in Eq. 1-6) with logistic growth without larval redistribution (i.e., with all larval produced locally are retained locally), the stepping-stone model becomes:

$$\frac{dN_{F,-S_F}}{dt} = r_F N_F - r_F \frac{N_F^2}{K_F} - (\mu_N + \mu_F) N_{F,-S_F} - D_F N_{F,-S_F} + \frac{D_F}{2} N_{F,-S_F+1} + \frac{D_M}{2} N_{M,S_M} \quad (S1)$$

$$\frac{dN_{F,i}}{dt} = r_F N_F - r_F \frac{N_F^2}{K_F} - (\mu_N + \mu_F) N_{F,i} - D_F N_{F,i} + \frac{D_F}{2} (N_{F,i-1} + N_{F,i+1}), \text{ where } i = -S_F + 1, \dots, -3, -2 \quad (S2)$$

$$\frac{dN_{F,-1}}{dt} = r_F N_F - r_F \frac{N_F^2}{K_F} - (\mu_N + \mu_F) N_{F,-1} - D_F N_{F,-1} + \frac{D_F}{2} N_{F,-2} + \frac{D_M}{2} N_{M,1} \quad (S3)$$

$$\frac{dN_{M,1}}{dt} = r_M N_M - r_M \frac{N_M^2}{K_M} - \mu_N N_{M,1} - D_M N_{M,1} + \frac{D_M}{2} N_{M,2} + \frac{D_F}{2} N_{F,-1} \quad (S4)$$

$$\frac{dN_{M,i}}{dt} = r_M N_M - r_M \frac{N_M^2}{K_M} - \mu_N N_{M,i} - D_M N_{M,i} + \frac{D_M}{2} (N_{M,i-1} + N_{M,i+1}), \text{ where } i = 2, 3, \dots, S_M - 1 \quad (S5)$$

$$\frac{dN_{M,S_M}}{dt} = r_M N_M - r_M \frac{N_M^2}{K_M} - \mu_N N_{M,S_M} - D_M N_{M,S_M} + \frac{D_M}{2} N_{M,S_M-1} + \frac{D_F}{2} N_{F,-S_F} \quad (S6)$$

in which r_F and r_M are intrinsic growth rates (per capita larval production) in the fishing grounds and MPA, and K_F and K_M are carrying capacities for cells in the fishing grounds and MPA respectively. All the other parameters are as defined in the main text. Although we initially write the model more generally (with habitat specific r_M , r_F , K_M and K_F), we explore the simpler case in which $r_M=r_F=r$ and $K_M=K_F=K$.

2.2. The two-patch box model for the closed system

When the MPA and fishing ground each have only one cell:

$$\frac{dN_F}{dt} = r_F N_F \left(1 - \frac{N_F}{K_F}\right) - (\mu_N + \mu_F) N_F - D_F N_F + D_M N_M \quad (\text{S7})$$

$$\frac{dN_M}{dt} = r_M N_M \left(1 - \frac{N_M}{K_M}\right) - \mu_N N_M - D_M N_M + D_F N_F \quad (\text{S8})$$

By re-parameterizing Eq. S1 and S2, the box model becomes:

$$\frac{dN_F}{dt} = r'_F N_F \left(1 - \frac{N_F}{K'_F}\right) - D_F N_F + D_M N_M \quad (\text{S9})$$

$$\frac{dN_M}{dt} = r'_M N_M \left(1 - \frac{N_M}{K'_M}\right) - D_M N_M + D_F N_F \quad (\text{S10})$$

where $r'_F = r_F - \mu_N - \mu_F$, $r'_M = r_M - \mu_N$, $K'_F = \frac{r_F - \mu_N - \mu_F}{r_F} K_F$, $K'_M = \frac{r_M - \mu_N}{r_M} K_M$. By assuming growth rate and carrying capacity are the same between the MPA and the fishing ground ($r_M = r_F = r$ and $K_M = K_F = K$), we have $\frac{K'_M}{K'_F} = \frac{r - \mu_N}{r - \mu_N - \mu_F}$.

By setting the differential mobility $\beta = \frac{D_F}{D_M}$, and the local effect $\rho = \frac{N_M^*}{N_F^*}$, we have the equilibrium solutions to Eq. S9 and S10:

$$N_M^* = K'_M \left(1 + \frac{\beta - \rho}{\rho r'_M} D_M\right) \quad (\text{S11})$$

$$N_F^* = K'_F \left(1 - \frac{\beta - \rho}{r'_F} D_M\right) \quad (\text{S12})$$

We find that ρ satisfies the following equation

$$G := D_M (\rho - \beta) \left(\frac{K'_F}{K'_M r'_F} \rho^2 + \frac{1}{r'_M} \right) + \left(\frac{K'_F}{K'_M} \rho - 1 \right) \rho = 0 \quad (\text{S13})$$

A positive root of ρ of Eq. S13 corresponds to a positive equilibrium if and only if $\rho > \beta - \frac{r'_F}{D_M}$

holds. Since G is a cubic polynomial in ρ and since $\rho = 0$ implies $G < 0$, it follows that Eq. S13

admits a positive root. Evaluating G for $\rho = \beta - \frac{r'_F}{D_M} > 0$, we find that $G = -\frac{r'_F}{r'_M} - \rho < 0$,

therefore there always exists a positive root ρ , which satisfies $\rho > \beta - \frac{r'_F}{D_M}$. Differentiating G by

ρ , we have:

$$\frac{\partial G}{\partial \rho} = \frac{D_M K'_F}{r'_F K'_M} \rho \left(\rho - \beta + \frac{r'_F}{D_M} \right) + \frac{D_M \beta}{r'_M \rho} + \frac{D_M K'_F}{r'_F K'_M} \rho^2 \quad (\text{S14})$$

When $\rho > 0$ and $\rho > \beta - \frac{r'_F}{D_M}$, we have $\frac{\partial G}{\partial \rho} > 0$. This implies that $G=0$ has a unique positive root ρ . Differentiating G by β or D_M , we have:

$$\frac{\partial G}{\partial \beta} = -D_M \left(\frac{K'_F}{r'_F K'_M} \rho^2 + \frac{1}{r'_M} \right) < 0 \quad (\text{S15})$$

$$\frac{\partial G}{\partial D_M} = (\rho - \beta) \left(\frac{K'_F}{r'_F K'_M} \rho^2 + \frac{1}{r'_M} \right). \quad (\text{S16})$$

$\frac{\partial G}{\partial D_M}$ has the same sign as $\rho - \beta$. If $\rho = \beta$, $G = \left(\frac{K'_F}{K'_M} \rho - 1 \right) \rho$, which has the same sign as

$\left(\frac{K'_F}{K'_M} \rho - 1 \right)$. If $\rho = \frac{K'_M}{K'_F}$, $G \sim \left(\frac{K'_M}{K'_F} - \beta \right)$ that has the same sign as $\left(1 - \frac{K'_F}{K'_M} \beta \right)$. Therefore, G always

changes sign between $\rho = \beta$ and $\rho = \frac{K'_M}{K'_F}$, and the root is always located in the corresponding

interval. Specifically, if $\rho > \frac{K'_M}{K'_F}$, $\rho \in \left(\frac{K'_M}{K'_F}, \beta \right)$, and if $\rho < \frac{K'_M}{K'_F}$, then $\rho \in \left(\beta, \frac{K'_M}{K'_F} \right)$.

Using implicit differentiation, we have

$$\frac{\partial \rho}{\partial \beta} = - \frac{\frac{\partial G}{\partial \beta}}{\frac{\partial G}{\partial \rho}} > 0 \quad (\text{S17})$$

$$\text{and } \frac{\partial \rho}{\partial D_M} = - \frac{\frac{\partial G}{\partial D_M}}{\frac{\partial G}{\partial \rho}} \quad (\text{S18})$$

So $\frac{\partial \rho}{\partial D_M}$ has an opposite sign of $\rho - \beta$, hence,

$$\frac{\partial \rho}{\partial D_M} < 0 \text{ when } \beta < \frac{K'_M}{K'_F} = \frac{r - \mu_N}{r - \mu_N - \mu_F} \quad (\text{S19})$$

$$\frac{\partial \rho}{\partial D_M} > 0 \text{ when } \beta > \frac{K'_M}{K'_F} = \frac{r - \mu_N}{r - \mu_N - \mu_F} \quad (\text{S20})$$

$$\frac{\partial \rho}{\partial D_M} = 0 \text{ when } \beta = \frac{K'_M}{K'_F} = \frac{r - \mu_N}{r - \mu_N - \mu_F} \quad (\text{S21})$$

The limiting values of ρ for low and high mobility are:

$$\lim_{D_M \rightarrow 0} \rho = \frac{K'_M}{K'_F} \text{ and } \lim_{D_M \rightarrow \infty} \rho = \beta \quad (\text{S22})$$

The limiting values of ρ for low and high differential movement β are:

$$\lim_{\beta \rightarrow 0} \rho = \rho_0 \text{ and } \lim_{\beta \rightarrow \infty} \rho = \infty \quad (\text{S23})$$

where ρ_0 in the case $D_M > r'_M$ and $\rho_0 > 0$ is the positive root of the quadratic form:

$$\frac{K'_F D_M}{K'_M r'_F} \rho^2 + \frac{K'_F}{K'_M} \rho + \frac{D_M}{r'_M} - 1 = 0 \text{ in the case } D_M > r'_M.$$

From S13, we have

$$\beta = \rho + \frac{\rho^2 K'_F - \rho K'_M}{\frac{K'_M D_M}{r'_M} + \frac{K'_F D_M}{r'_F} \rho^2} \quad (\text{S24})$$

So, from S11 and S12, we have:

$$N_M^* + N_F^* = K'_F K'_M \frac{(r'_M \rho + r'_F)(1 + \rho)}{r'_M K'_F \rho^2 + r'_F K'_M} \quad (\text{S25})$$

Therefore,

$$\frac{\partial(N_M^* + N_F^*)}{\partial \rho} > 0 \text{ when } \rho < \rho^* \text{ (equivalent to } \frac{\partial(N_M^* + N_F^*)}{\partial \beta} > 0 \text{ when } \beta < \beta^* \text{ due to S17)} \quad (\text{S26})$$

$$\text{and } \frac{\partial(N_M^* + N_F^*)}{\partial \rho} < 0 \text{ when } \rho > \rho^* \text{ (equivalent to } \frac{\partial(N_M^* + N_F^*)}{\partial \beta} < 0 \text{ when } \beta > \beta^*) \quad (\text{S27})$$

where ρ^* is the root of quadratic equation as follows:

$$(r'_M + r'_F) r'_F K'_M + 2 r'_M r'_F (K'_M - K'_F) \rho - (r'_M + r'_F) r'_M K'_F \rho^2 = 0 \quad (\text{S28})$$

When $\rho = \frac{K'_M}{K'_F}$, $N_M^* + N_F^* = K'_M - K'_F$.

Since $\rho^* < \frac{K'_M}{K'_F}$, so $\max(N_M^* + N_F^*) > K'_M - K'_F$.

Using implicit differentiation, we have:

$$\frac{\partial(N_M^* + N_F^*)}{\partial D_M} = - \frac{\frac{\partial(N_M^* + N_F^*)}{\partial \rho}}{\frac{\partial D_M}{\partial \rho}} \quad (\text{S29})$$

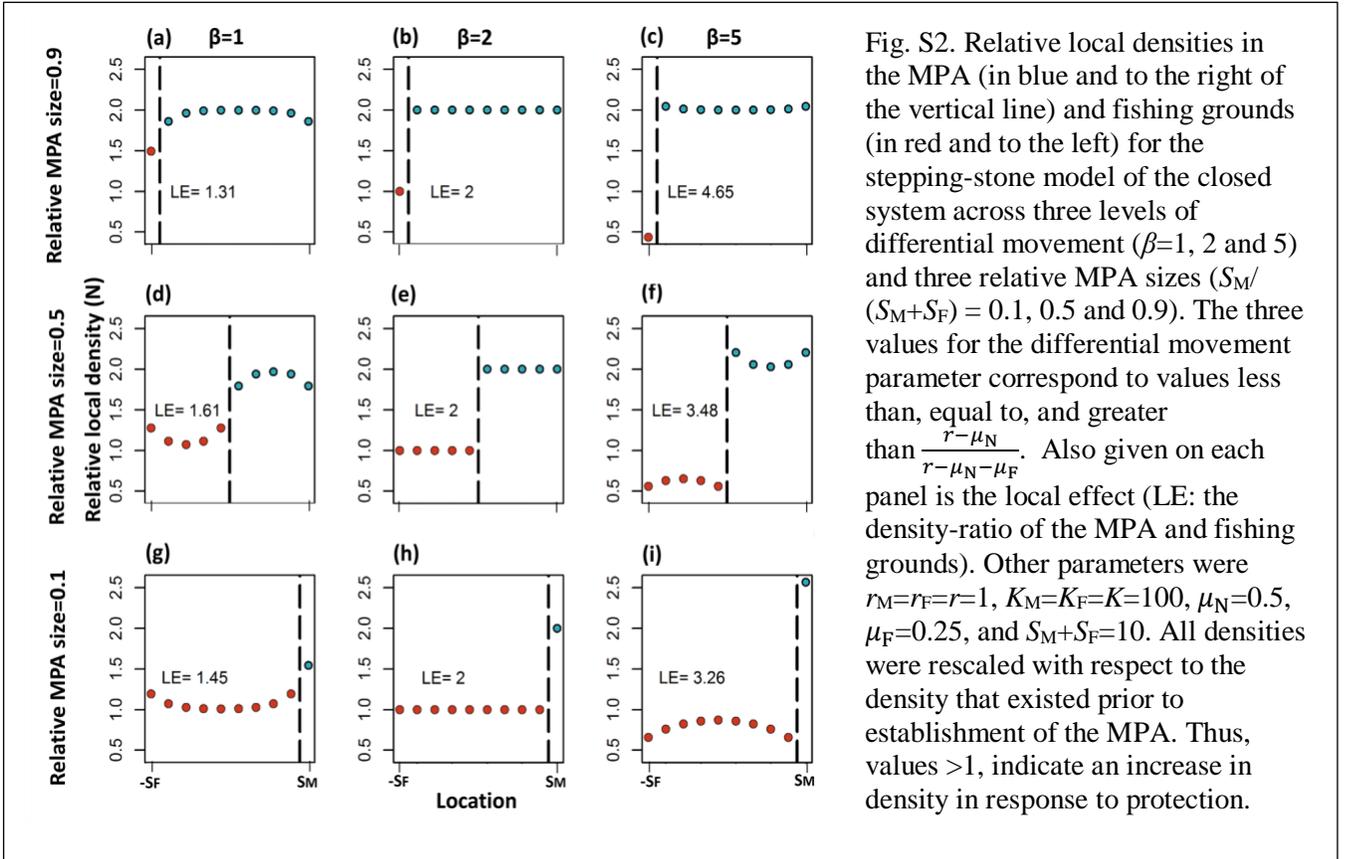
Based on S22, S23 and S29, we know that when $\beta > \rho^*$, $N_M^* + N_F^*$ would monotonically change with D_M , but when $\beta < \rho^*$, $N_M^* + N_F^*$ is unimodal with D_M .

$$\text{While } N_F^* = K_F' \left[1 - \frac{D_M(\beta - \rho)}{r_F'} \right] = K_F' - \frac{\rho^2 K_F' - \rho K_M'}{\frac{K_M' r_F'}{K_F' r_M'} + \rho^2}, \quad (\text{S30})$$

$$\text{So } \frac{\partial N_F^*}{\partial \beta} < 0. \quad (\text{S31})$$

2.3 The stepping stone model for the closed system

We simulated densities across the entire study region (Fig. S2). Spatial patterns of density are similar to those seen with the open system, except that the critical value for the differential mobility β in the closed system is determined by the value of $\frac{K_M'}{K_F'} = \frac{r - \mu_N}{r - \mu_N - \mu_F}$ instead of $(\mu_N + \mu_F)/\mu_N$ (see Eq. S19-S21). Here this critical value is $\beta=2$.



SECTION 3: SEMI-CLOSED SYSTEM (LOGISTIC GROWTH WITH LARVAL REDISTRIBUTION)

3.1 *The basic model*

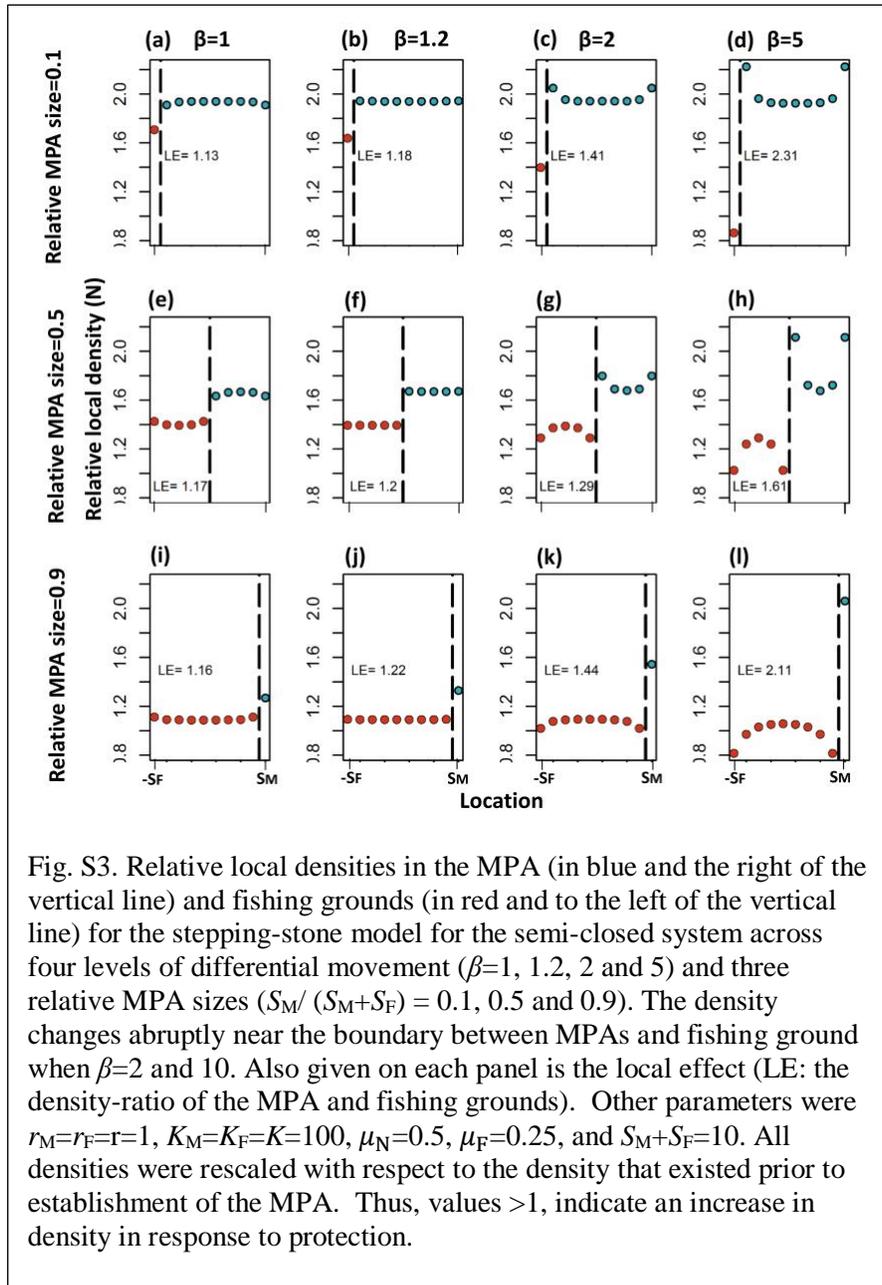
The previous two models represent ends of a spectrum. At one extreme, in the open system (constant larval rain) the MPA-fishing ground system is small relative to the dispersal scale of larval, and as a result, adults in the MPA-fishing ground system have no effect on the supply of larvae to the study system. At the other extreme, in the closed system (logistic growth without larval redistribution), each cell is large relative to the scale of larval dispersal, and as a result, larvae produced by the local adults are retained locally (there is no larval dispersal). Our third case is intermediate. We assume that the MPA-fishing ground system is closed (i.e., more closed than the open system) but that larvae produced in the system are well mixed (i.e., more open than the closed system). To model the semi-closed system, we assume that larvae settle uniformly across the system with the total input of larvae resulting from the summed reproduction across all cells. Thus, we replace $r_i N_i$ in Eqs. S1-S6 by:

$$\frac{1}{S_M+S_F} \left(r_F \sum_{i=-S_F}^{-1} N_{F,i} + r_M \sum_{i=1}^{S_M} N_{M,i} \right) \quad (\text{S32})$$

3.2 *The stepping stone model for the semi-closed system*

Solutions to the model for the semi-closed system (even with only two patches) are more complex than for the other two cases. Therefore, we present only simulation results, and focus on the stepping-stone version of the model ($S_M+S_F=10$) here. The spatial patterns in density along the MPA-fishing ground system (Fig. S3) were similar to those obtained for the other two models in the absence of differential movement ($\beta=1$) and for large degrees of differential movement ($\beta>2$). However, the critical value of β at which differential movement just offsets the spill-over potential was different from the other two models. In the model for the open

system, the critical value occurred at $(\mu_N + \mu_F)/\mu_N$ (i.e., $\beta=1.5$ for the case shown in Fig. S1), whereas in the model for the closed system, the critical value occurred at $\beta = \frac{r-\mu_N}{r-\mu_N-\mu_F}$ (i.e., at $\beta=2$ for the case that was simulated in Fig. S2). Here, in the presence of larval redistribution (i.e., the semi-closed system), the critical value was even smaller. Based upon simulation, we found this critical value to be ~ 1.2 (Fig. S3). Thus, compared to the closed system, larval

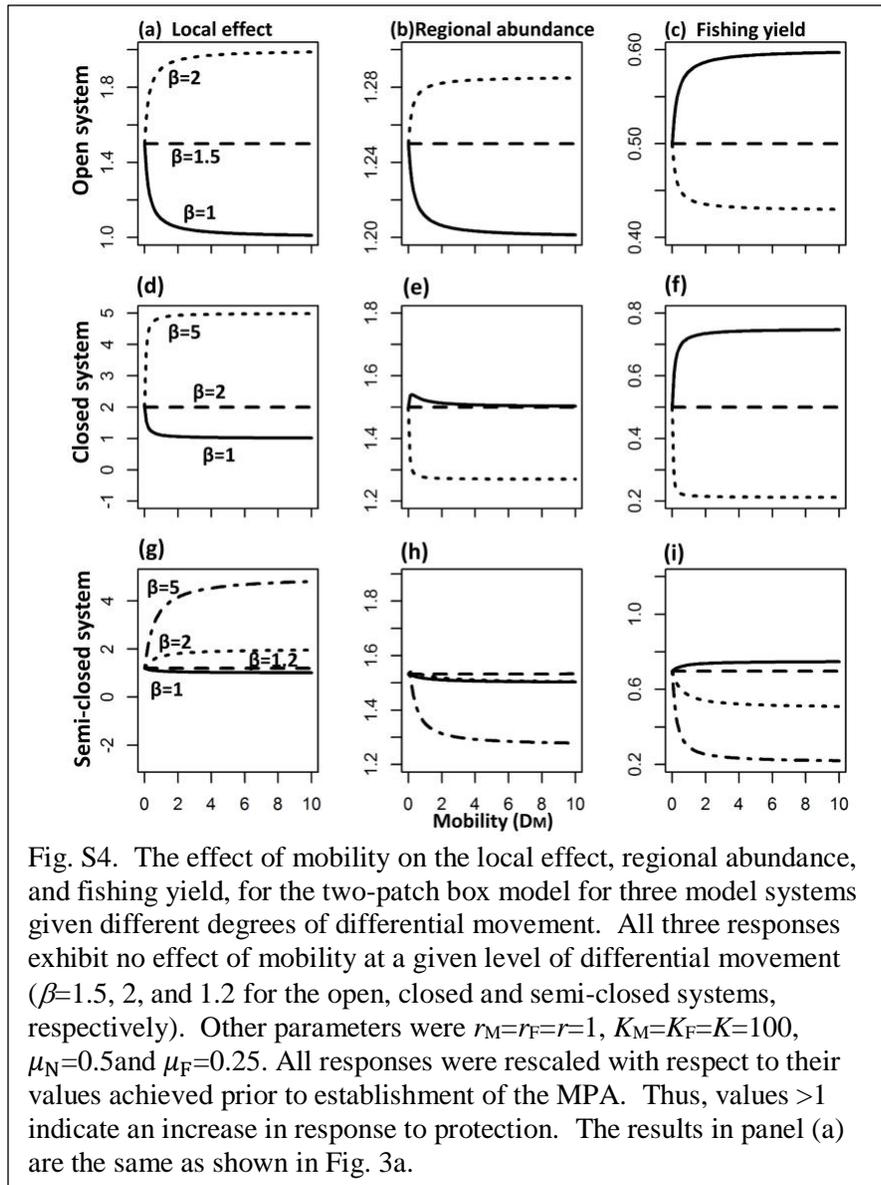


redistribution across the MPA and fishing grounds reduced the degree of differential movement required to transition from a gradual to an abrupt change in density across the MPA-fishing ground border.

SECTION 4: LOCAL EFFECT, REGIONAL ABUNDANCE, AND FISHING YIELD

The above analyses emphasize the spatial pattern of densities and how it is modified by differential movement. Here we compare results for the three systems with respect to effects of mobility and fishing mortality on the local effect, regional abundance, and fishing yield.

4.1 Effects of mobility



As illustrated above, results from the three systems (open, closed, and semi-closed) yielded similar qualitative results as mobility increased in the two-patch box model (Fig. S4). At the critical values of differential movement, β , all three indices (local effect, regional abundance, and fishing yield) were independent of mobility (see the horizontal dashed lines in Fig. S4). When β was smaller than

the critical values, the spill-over pattern dominated: the local effect decreased but the fishing

yield increased with overall mobility. When β was larger than the critical values, these trends were reversed.

In the open system, regional abundance increased with differential mobility β and its relationship with overall mobility shifted from negative to positive as β increased above its critical value (Fig. S4b). However, the regional abundance in closed and semi-closed systems showed more complicated patterns due to effects of logistic growth (Fig 4e,h).

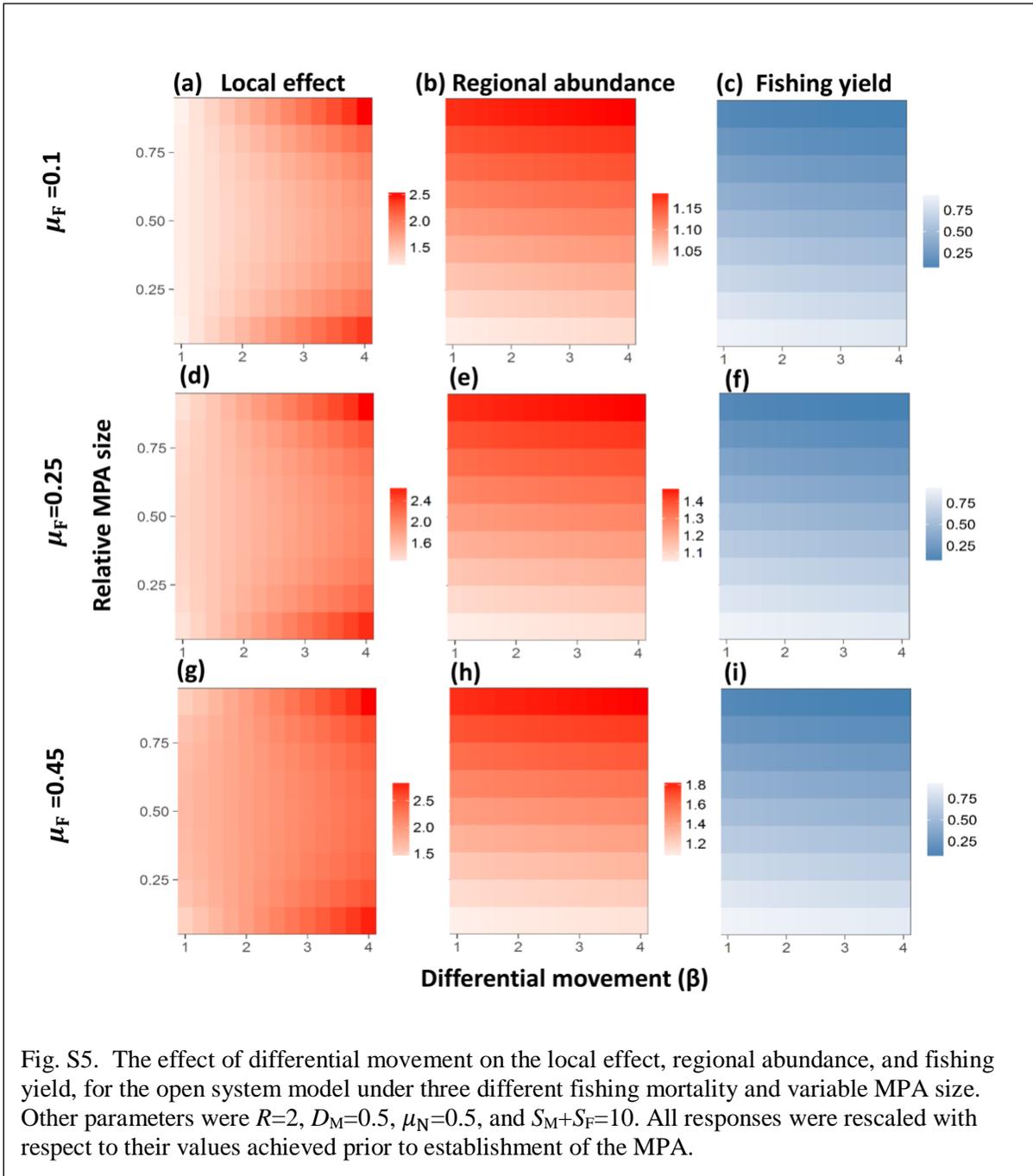
4.2 Effects of fishing mortality

A full analysis of the interplay between different movement, fishing mortality and MPA size is beyond the scope of this paper. Here, we only show simulated results of the three indices under three levels of fishing mortalities and highlight several key results regarding the effect of differential movement (Fig. S5-S7):

- i) Increasing differential movement increased the local effect in all three models for all MPA sizes and all fishing mortalities.
- ii) Increasing differential movement tended to either decrease, or have minimal effect on, the regional abundance.
- iii) Increasing differential movement usually reduced fishing yield.

The effect of differential movement on the local effect and on fishing yield is most easily understood by considering that differential movement drives individuals from the fishing grounds into the MPA. As a result, the local effect increases (because density in the MPA is increased relative to the fishing grounds) and fishing yield usually decreases as fish move at greater rates into the protected area. Notice that the effect of increased differential movement on the local effect holds across all levels of MPA size and fishing mortality and the effect on fishing

yield holds across most of these levels (there is a slight increase in fishing yield with increased differential movement when fishing mortality is large and the MPA is small in the closed and semi-closed system: see Fig. S6 and S7). Thus, beneficial effects of MPAs on fisheries are less likely when the target organism exhibits a greater degree of differential movement.



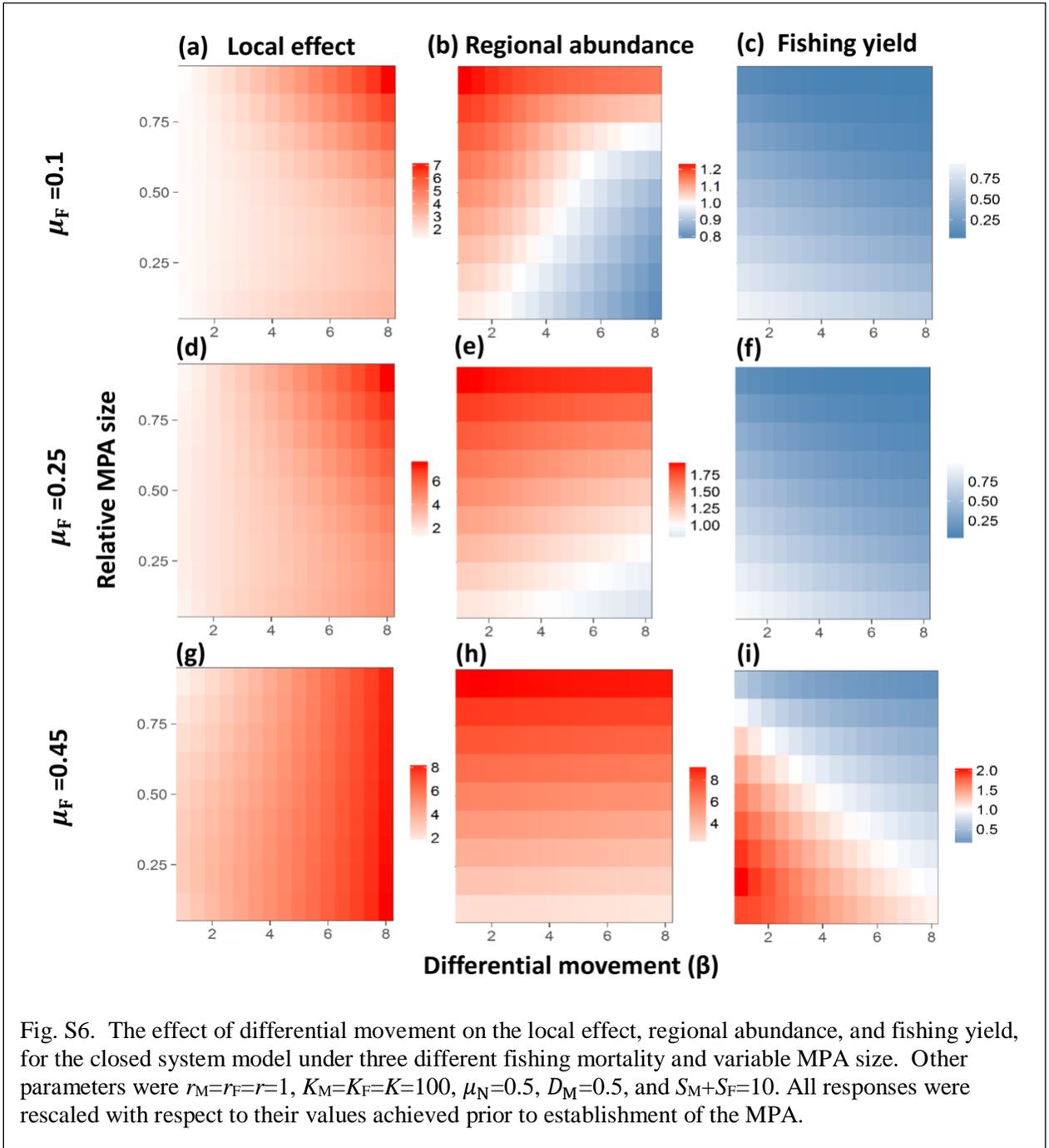


Fig. S6. The effect of differential movement on the local effect, regional abundance, and fishing yield, for the closed system model under three different fishing mortality and variable MPA size. Other parameters were $r_M=r_F=r=1$, $K_M=K_F=K=100$, $\mu_N=0.5$, $D_M=0.5$, and $S_M+S_F=10$. All responses were rescaled with respect to their values achieved prior to establishment of the MPA.

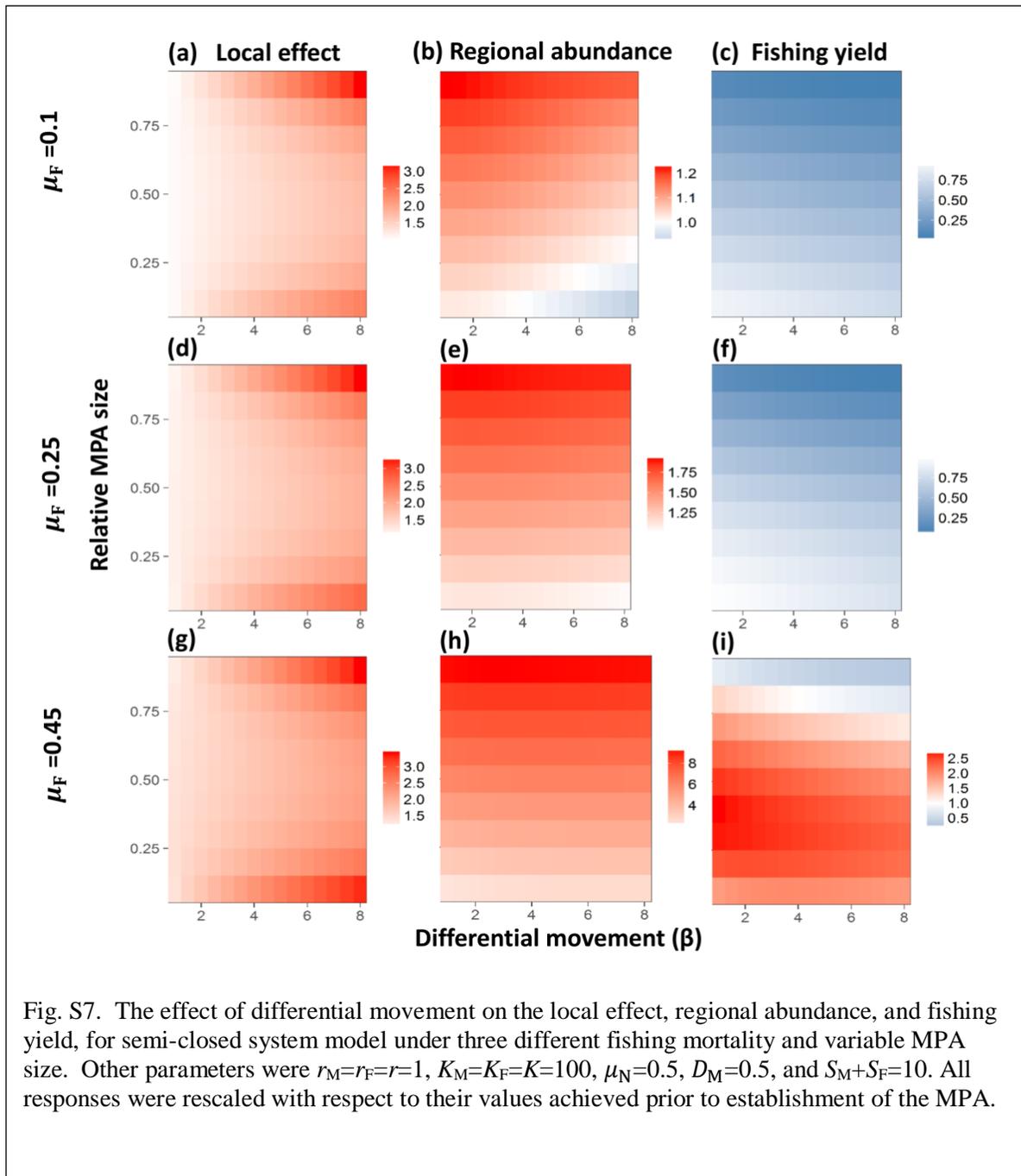


Fig. S7. The effect of differential movement on the local effect, regional abundance, and fishing yield, for semi-closed system model under three different fishing mortality and variable MPA size. Other parameters were $r_M=r_F=r=1$, $K_M=K_F=K=100$, $\mu_N=0.5$, $D_M=0.5$, and $S_M+S_F=10$. All responses were rescaled with respect to their values achieved prior to establishment of the MPA.