

Random movement of predators can eliminate trophic cascades in marine protected areas

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Abstract. The protection of predators inside marine reserves is expected to generate trophic cascades with predator density increasing but prey density decreasing; however, predators and prey often both increase inside reserves. This mismatch between the expected and observed change in prey density has been explained because prey also are harvested; that is, the protection of prey compensates for the additional predation inside the reserve. Here, we show that this mechanism alone cannot increase densities of predator and prey; other mechanisms are required, and we hypothesized that movement of predator and/or prey might provide such a mechanism. We therefore built two spatially implicit two-patch predator-prey models with movement of predator and prey between reserve and fishing grounds. We show that post-settlement movement of predators (but not prey) altered the strength of trophic cascades and could increase densities of both predator and focal prey. We further built a more general model that shows that predator post-settlement movement can reinforce and even supplement the effect of two previously investigated mechanisms producing trophic cascades: a prey size refuge and predator density-dependent mortality. Our study increases understanding of mechanisms that can alter the strength (and direction) of prey responses inside marine reserves and highlights the importance of movement in human-induced heterogeneous systems.

Key words: marine reserves; model; post-settlement movement; predation; trophic interaction.

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INTRODUCTION

Marine reserves, or marine protected areas (MPAs), are established, in part, to increase densities of populations and enhance biodiversity in marine ecosystems (Allison et al. 1998, Palumbi 2001, 2002). However, the effects of MPAs vary among species with different trophic niches, body sizes, and life histories (Micheli et al. 2004a, Guidetti and Sala 2007). The strongest beneficial effects of MPAs are typically seen for large predators—species that are targeted by commercial and recreational fisheries (Pauly et al. 1998, Jackson et al. 2001, Micheli et al. 2004b, Claudet et al. 2010). The increased density of

large predators inside MPAs should lead to trophic cascades; for example, due to the increase in predators, herbivores should be less abundant, and primary producers should be more abundant, inside MPAs (Pinnegar et al. 2000, Shears and Babcock 2002, Daskalov et al. 2007).

The evidence for trophic cascades in MPAs is mixed. In some cases, prey decrease in response to protection (Sala and Zabala 1996, Ruckelshaus and Hay 1998), but in other cases, prey increase following protection (Sala 1997, Guidetti 2006, Guidetti and Sala 2007). Meta-analyses, which should help resolve this heterogeneity, also give equivocal results (e.g., Halpern 2003, Micheli et al. 2004b, Guidetti and Sala 2007, Lester et al.

2009). Theoretical and empirical studies have suggested several possible explanations for weakened trophic cascades; for example, predators may shift to other prey (Kellner et al. 2010), food webs may be reticulate (Strong 1992, Fox and Olsen 2000), pathogens may become more abundant and reduce predator density (Andrew 1991), or intraspecific competition may reduce the size of predators thereby reducing their feeding rates on prey (Guidetti 2006).

Two other important potential explanations were suggested by Mumby et al. (2006) based upon their study of the Exuma Cays Land and Sea Park in the Caribbean (ECLSP). Mumby et al. (2006) suggested that if large size prey could escape predation (i.e., had a prey size refuge), the magnitude of the trophic cascade would be reduced. This hypothesis was supported theoretically by Baskett (2006). Mumby et al. (2006) also suggested that prey (i.e., herbivores) also were killed by fishers (either for food or indirectly as bycatch), and thus, MPAs simultaneously released herbivores as well as piscivores from fishing. If fishing on herbivores was strong enough, then the benefit of protection could overwhelm the effect of the trophic cascade, leading to a net increase in herbivores inside the MPA. Although this mechanism has been incorporated in models that also involve other mechanisms (e.g., size refuge [Baskett 2006], generalist predator with density-dependent mortality [Kellner et al. 2010]), the effect of this mechanism has not been investigated in isolation.

Below we develop a predator-prey model to show that the reduction of fishing on prey alone is insufficient (in the absence of other mechanisms) to negate the expected trophic cascade in an MPA. We then develop models of predator movement, which can lead to the increases in predator and prey densities in MPAs (when combined with the fishing mechanism). We focus on a system with a single predator and single prey (i.e., in which the predator is a specialist), but later demonstrate that the qualitative results also hold for a system in which there is an alternative prey (i.e., in which the predator is a generalist). Finally, we develop a comprehensive model including previously proposed mechanisms (a prey size refuge and density-dependent mortality in the predator), as well as predator movement, to evaluate the relative

influence and possible interactions among these three mechanisms. All the model simulations in this study were implemented in the program R 3.1.1 (R Core Team 2014).

A PREDATOR-PREY MODEL: ISOCLINE ANALYSIS

To evaluate the hypothesis that harvesting of the prey can switch the response of prey inside an MPA from negative (expected from a trophic cascade) to positive, we built a simple predator-prey model based upon the Lotka-Volterra model but with additional terms for fishing mortality for the predator and prey, as well as density-dependent mortality of the prey:

$$\frac{dN}{dt} = rN - eN^2 - \mu_N N - aNP - bF_N N \quad (1)$$

$$\frac{dP}{dt} = caNP - \mu_P P - bF_P P \quad (2)$$

where N and P are the densities of prey and predator respectively, r is the per capita growth rate of the prey in the absence of the predator, e is the effect of intraspecific competition on prey survival, μ and F are the natural and fishing-induced mortality rates of the prey or predator (indicated with subscripts N or P), a and c are the predator's attack rate and conversion efficiency, and b indicates whether the system is fished (e.g., before creation of an MPA: $b = 1$) or protected (i.e., inside the MPA: $b = 0$). We restrict our analyses to the parameter values that lead to positive equilibrium densities of the predator and prey before establishing the MPA (i.e., both species persist globally in the presence of fishing).

Given the above, the solution of Eqs. 1 and 2 is:

$$N^* = \frac{\mu_P + bF_P}{ca} \quad (3)$$

$$P^* = \frac{ca(r - \mu_N) - cabF_N - e(\mu_P + bF_P)}{ca^2} \quad (4)$$

from which we can draw a phase plane for the system before vs. after establishment of the MPA (Fig. 1a). Reduction of fishing pressure (i.e., establishment of an MPA, indicated by the solid lines) will cause the prey isocline to shift upwards (toward greater P for a given N) and the predator isocline to shift to the left (to lower N for a given P). As a result, the equilibrium predator

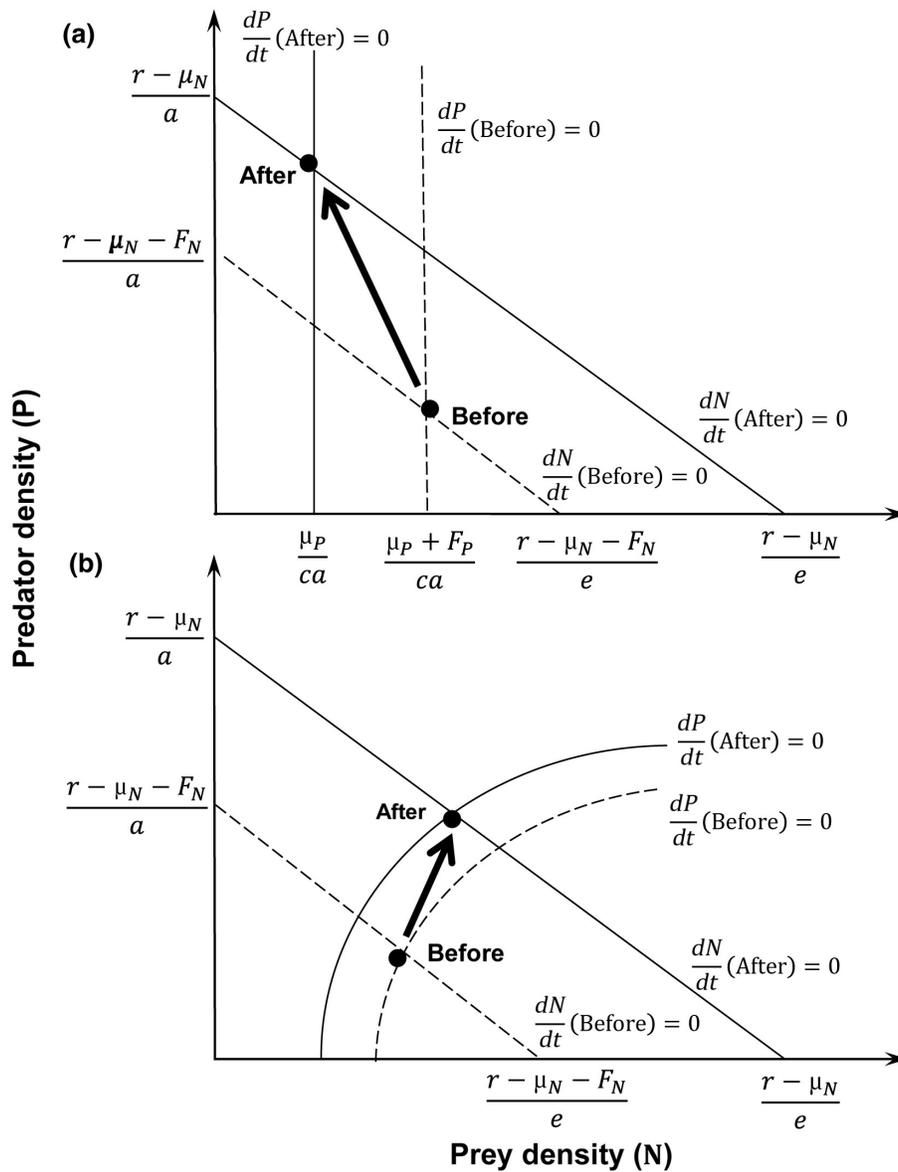


Fig. 1. Phase planes and no-growth isoclines for the predator-prey system before and after establishment of a marine protected area (MPA). (a) If predators exhibit a type I functional response and prey compete intraspecifically, the creation of an MPA shifts the predator isocline to the left and the prey isocline upward, resulting in an increase in the equilibrium predator density but a decrease in prey density. Thus, creation of an MPA results in a trophic cascade. (b) If the predator’s isocline “slants to the right” (Mittelbach et al. 1988) due to predator interference or other mechanisms, then creation of an MPA can increase the density of both the predator and prey; that is, a trophic cascade is no longer expected.

population always increases following protection (i.e., $\partial P^*/\partial F_P = -eb/ca^2 < 0$ and $\partial P^*/\partial F_N = -b/a < 0$) and the equilibrium prey population always decreases (i.e., $\partial N^*/\partial F_P = b/ca > 0$); that is, there is always a trophic cascade (Fig. 1a). Note that this

qualitative pattern does not depend on the magnitude of the fishing mortality on prey (i.e., the above sensitivities do not depend on F_N ; in addition, $\partial N^*/\partial F_N = 0$). In addition, altering the predator’s functional response from a type I to a type II

or III also would not change this pattern, because the predator isocline would remain vertical.

As a consequence of the above analysis, fishing on prey is an insufficient explanation for the observed increase in prey density in MPAs; that is, there must be other mechanisms operating to produce deviations from the classical trophic cascade pattern. In the above phase-plane framework, the only way to achieve increased prey densities after protection is to have a predator isocline that “slants to the right” (Mittelbach et al. 1988, e.g., due to some form of predator interference), in combination with fishing mortality on the prey (Fig. 1b). If the “slant” in the predator isocline is sufficient, both predator and prey density can increase after a site is protected. A variety of mechanisms can produce this “slant” of the predator isocline, for example, cannibalism, territoriality, ratio dependence, limitation by another resource, stage-structured dynamics, or the form of predator density-dependent mortality (Mittelbach et al. 1988, Kellner et al. 2010). Here, we hypothesize that post-settlement movement of the predator and/or prey might also lead to similar patterns and result in departures from predictions of trophic cascade theory. We therefore relax our assumption about independence of the MPA from the fishing ground by adding in movement of predator and prey between fishing grounds and the MPA to determine how movement can alter resulting patterns of predator and prey densities following protection (in the absence of predator interference).

MOVEMENT OF PREDATOR AND PREY

Spatial connectivity in marine systems is often modeled via larval connectivity (e.g., Kinlan and Gaines 2003, Cowen et al. 2006, Cowen and Sponaugle 2009). Yet, post-settlement movement also can play an important role in the response of species to protection (Moffitt et al. 2009, Claudet et al. 2010, Grüss et al. 2011, Langebrake et al. 2012). More generally, movement is known to affect species interactions and food web structure in meta-communities (deRoos et al. 1991, Mccauley et al. 1996, Barraquand and Murrell 2013, Jeltsch et al. 2013). For example, predators moving from one patch could produce strong cascades in the adjacent patch (Casini et al. 2012). However, whether and how movement,

especially post-settlement movement, can influence trophic cascade patterns in MPAs is still unknown. We build two predator–prey models with random movement between the MPA and fishing ground to evaluate how movement can alter the resulting predator–prey patterns.

Specialist predator (one-prey) model with movement

We first built a spatially implicit model with two discrete patches (patch M for the MPA and patch F for the fishing grounds) to study a one-predator–one-prey system in which movement coupled the dynamics of the two patches. We considered the prey to be an herbivore (as in Mumby’s original formulation), but did not explicitly consider algal dynamics (a sessile resource in most reef systems; Kinlan and Gaines 2003). Instead, we included the effects of the herbivore–algae interaction via a density-dependent mortality rate for the herbivores (i.e., prey). Our model incorporated logistic growth of the prey, larval connectivity, post-settlement movement, and natural and fisheries-induced mortality:

$$N_M = r_N[(1-p)N_M + pN_F] - eN_M^2 - \mu_N N_M - a_N N_M P_M + m_N(N_F - N_M) \quad (5)$$

$$P_M = c[(1-p)a_N N_M P_M + p a_N N_F P_F] - \mu_P P_M + m_P(P_F - P_M) \quad (6)$$

$$N_F = r_N[(1-p)N_F + pN_M] - eN_F^2 - \mu_N N_F - a_N N_F P_F + m_N(N_M - N_F) - F_N N_F \quad (7)$$

$$P_F = c[(1-p)a_N N_F P_F + p a_N N_M P_M] - \mu_P P_F + m_P(P_M - P_F) - F_P P_F \quad (8)$$

where the state variables N_M , N_F , P_M , and P_F are the densities of prey and predator in the MPA and the fishing ground respectively, and all parameters are defined in Table 1.

We used both analytic and numeric methods to study the influence of movement. We first studied the separate influences of the movement of only the predator or prey (i.e., when either $m_N = 0$ or $m_P = 0$) on the strength and occurrence of a trophic cascade. We did not include larval connectivity in these analyses because this simplification allowed us to obtain analytic solutions (see Appendices S2 and S3). We then simulated

Table 1. Variables and parameters used in the models.

Symbol	Definition	Default value†	Range	Reference(s)
State variables				
N	Focal prey density			
N_S	Small size focal prey density			
N_L	Large size focal prey density			
P	Predator density			
S	Alternative prey density			
Parameters				
m_N	Focal prey movement rate		0–1	
m_P	Predator movement rate		0–1	
m_S	Alternative prey movement rate		0–1	
a_N	Attack rate on focal prey	0.04/P/yr		Kellner et al. (2010)
a_S	Attack rate on alternative prey	0.05/P/yr		Kellner et al. (2010)
a_{N_S}	Attack rate on small size focal prey	0.04/P/yr		Kellner et al. (2010)
a_{N_L}	Attack rate on large size focal prey		0–0.003 or 0–0.02/P/yr	
γ	Maturation rate of focal prey	0.447/yr		Choat et al. (2003)
c	Predator conversion efficiency	0.0175/PN		Baskett (2006)
r_N	Growth rate of focal prey	2.5/yr		Froese and Pauly (2014) (accessed 31 May 2014)
r_S	Growth rate of alternative prey	1.36/yr		Kellner et al. (2010)
μ_N	Natural mortality rate of focal prey	0.11/yr		Choat et al. (2003)
μ_S	Natural mortality rate of alternative prey	0.11/yr		Choat et al. (2003)
μ_P	Natural mortality rate of predator	0.0345/yr		Sadovy and Eklund (1999)
e	Density-dependent mortality rate of prey	0.02/N/yr		Osenberg et al. (2002)
e_P	Density-dependent mortality rate of predator		0–0.02/N/yr	
p	Proportion of larval exchanged between patches	0	0–0.393	Cowen et al. (2006)
F_N	Fishing mortality on focal prey	0.2	0–1.5/yr	
F_S	Fishing mortality on alternative prey	qF_N	$0.5 F_N$	Kellner et al. (2010)
F_P	Fishing mortality on predator	0.005, 0.02	0–0.06/yr	

† P and N indicate the same units in which predator and prey density were measured (i.e., no./m²).

the dynamics of the full system to investigate the combined effects of the movement of both the predator and prey in the absence of larval connectivity, and the combined effects of predator movement and larval connectivity without prey movement. To evaluate the influence of the MPA, we quantified the difference between the prey (or predator) density in the MPA (i.e., after establishing the MPA) vs. the density of the prey (or predator) in the fishing grounds before the MPA was established. Before building the MPA, we obtained the densities in the fishing ground by setting both m_N and $m_P = 0$ in Eqs. 7 and 8. This yielded the “before” solution: N_0^* and P_0^* . After building the MPA, the densities in the MPA site (i.e., the “after data”) were obtained by solving Eqs. 5 and 6. This yielded N_M^* or P_M^* . Because predator density always increased after building the MPA (e.g., $\partial P^* / \partial F_P = -eb/ca_N^2 < 0$ from Eq. 4), we mainly focused on the change of prey density

before and after the MPA establishment. We were primarily interested in determining whether specific movement parameters (m_N and m_P) under different fishing mortality combinations (F_N and F_P) could negate the trophic cascade and thus increase both predator and prey densities after MPA establishment.

Analytic approach: only prey move.—If the predator was sedentary ($m_P = 0$) and there was no larval connectivity ($p = 0$), but the prey was mobile, then as the prey’s movement rate (m_N) increased, the predator’s density in the MPA increased linearly (Fig. 2b) but the prey’s density remained constant (Fig. 2a). The constant prey density occurred because the prey density in the MPA was set by the predator’s natural mortality, which was constant: In the absence of predator movement, the prey density equilibrated at the density required to generate a predator birth rate that balanced the predator’s mortality rate (e.g.,

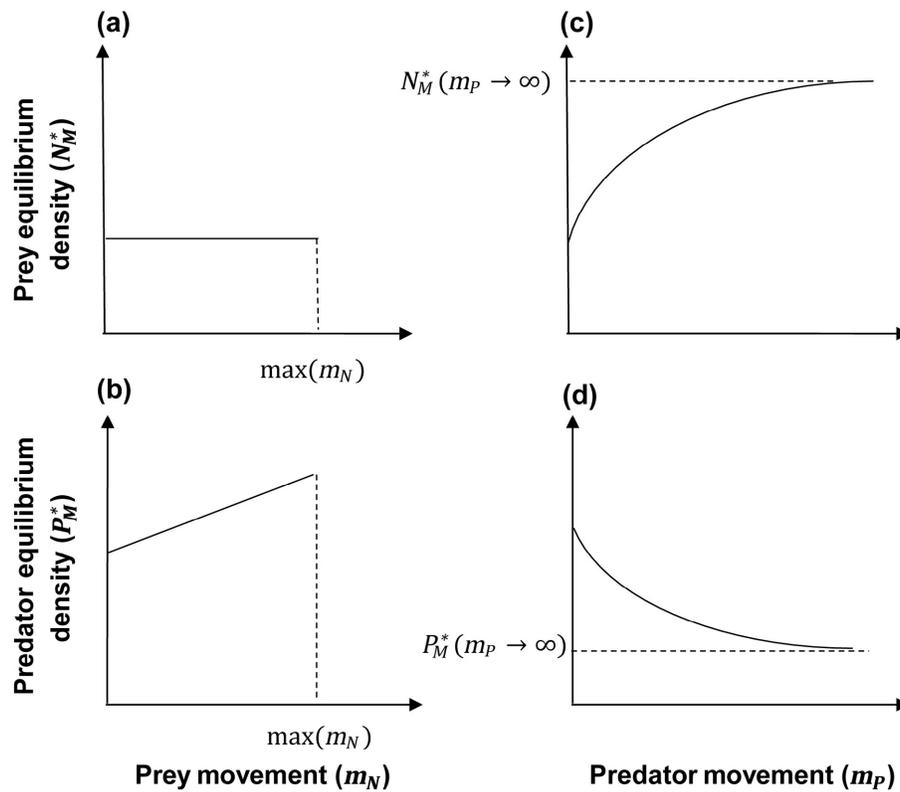


Fig. 2. Results for the specialist predator model (one-predator–one-prey model): effect of movement rate of predator or prey (m_p or m_N) on the equilibrium densities in the marine protected area (MPA), in the absence of larval connectivity ($p = 0$). (a) Prey equilibrium density (N_M^*) is independent of prey movement rate (m_N) up to $\max(m_N)$, at which point both the predator and prey go extinct; (b) predator equilibrium density (P_M^*) linearly increases with the increase in prey movement rate (m_N) up to $\max(m_N)$; (c) prey equilibrium density (N_M^*) increases with the increase in predator movement rate (m_p), up to an asymptote $N_M^*(m_p \rightarrow \infty)$; (d) predator equilibrium density (P_M^*) decreases to an asymptote $P_M^*(m_p \rightarrow \infty)$ as predator movement rate (m_p) increases. Detailed functions are Eqs. 34–35 and 50–51 in Appendices S2 and S3.

Oksanen et al. 1981). Without prey movement ($m_N = 0$), prey density in the fishing ground was higher than in the MPA (compare Eqs. 30 and 32 in Appendix S2); that is, there was a trophic cascade. In the presence of prey movement, prey mixed between the MPA and fishing ground, but this influx of prey into the MPA increased predator density, and this increased mortality of the prey prevented an increase in prey density in the MPA. As prey movement increased even further, the MPA became a larger prey sink and the mortality on prey in the MPA imposed by the protected and subsidized predator population eventually (i.e., at $\max [m_N]$) caused the global extinction of the prey. The collapse of prey led to the collapse of predator. Thus, when only prey

moved, creation of an MPA led to an increased predator density but could not also lead to increased densities of prey.

Analytic approach: only predators move.—In contrast, if the predator moved but the prey was sedentary ($m_N = 0$) and there was no larval connectivity ($p = 0$), then as the predator’s movement (m_p) increased, predator density decreased in the MPA (Fig. 2d; Eq. 51 in Appendix S3), eventually converging to $P_M^*(m_p \rightarrow \infty)$; that is, without movement, the MPA protected the predator, but greater predator movement homogenized the predator density across the entire landscape, elevating predator density in the fishing grounds and reducing predator density in the MPA. As a result of the decrease in

predator density in the MPA, prey density increased to a maximum (Fig. 2c; Eq. 52 in Appendix S3).

Thus, predator movement caused predator densities to decrease, but prey densities to increase, in the MPA. However, predator densities were always higher in the MPA than they were before the creation of the MPA. The question then is whether the positive effect of predator movement on prey made prey density higher in the MPA than it was before creation of

the MPA. If so, then the trophic cascade pattern could be reversed. To fully visualize this question, we examined how the effect of the MPA on prey (the difference in prey density from before to after) varied depending on the fishing rates on the predator and prey for several predator movement rates (Fig. 3; see also Appendix S3: Fig. S1). When predator movement was 0, prey density always declined following protection (Fig. 3a and Appendix S1: Fig. S1; as in Fig. 1a); that is, there was a trophic cascade. At greater predator

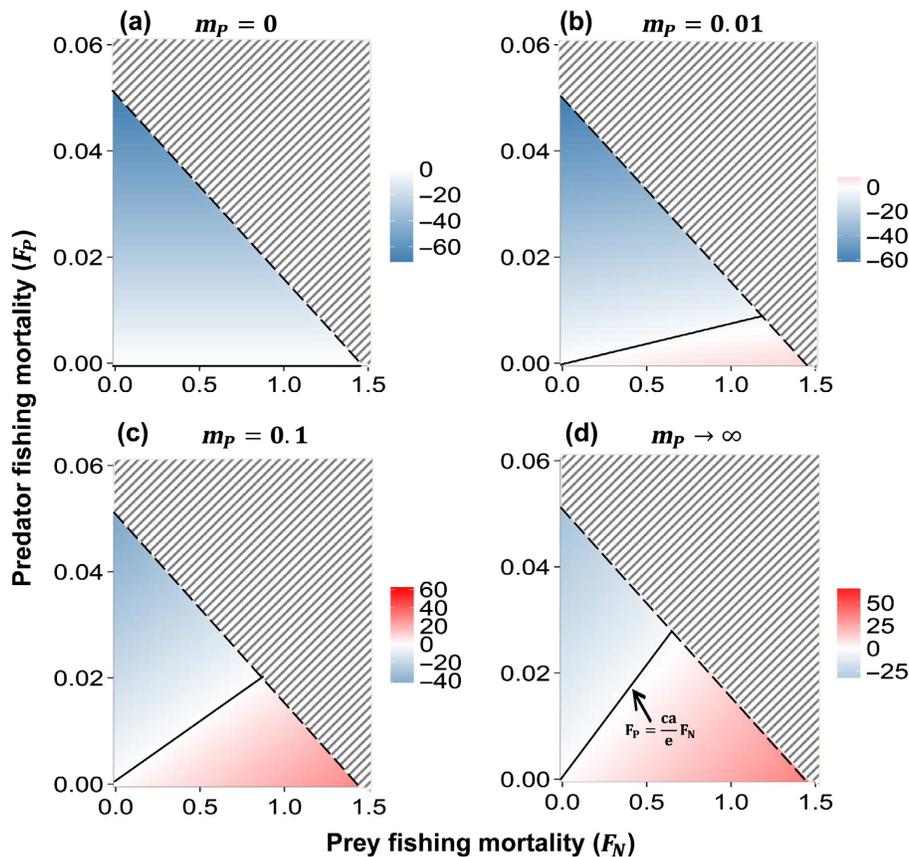


Fig. 3. Results for the specialist predator model (one-predator-one-prey model): change in prey equilibrium density after building the marine protected area (MPA) for four predator movement rates ($m_p = 0, 0.01, 0.1,$ and ∞/yr) under different combinations of fishing rates (F_p and F_N) with $m_N = 0$ and $p = 0$. The black dashed line separates the parameter space in which predators are extinct before building the MPA (hatched area) vs. the parameter space in which both species are extant (area below the hatched area). Colors below this dashed line indicate the change in prey density after establishment of the MPA: red indicates that prey density increased, whereas blue indicates that prey density decreased. The solid black line delineates the parameter space in which the trophic cascade occurs (blue) or is reversed (red). The slope of this line increases with an increase in predator movement, approaching ca_N/e as $m_p \rightarrow \infty$. Other parameters and calculations are given in Table 1 and Appendices S1 and S3.

movement rates, there were some combinations of fishing mortalities that reversed the trophic cascade (Fig. 3b–d). The F_P – F_N parameter space that reversed the trophic cascade increased in size as predator movement increased (compare 3b with c with d; see Eq. 56 in Appendix S3). Under these combinations (e.g., $F_P/F_N < ca_N/e$ when m_P is large), predator movement led to increased densities of both the predator and prey after creation of the MPA.

Therefore, an increase in predator movement (m_P), but not prey movement, can lead to beneficial effects on prey that can negate the expected trophic cascade pattern in the MPA.

Simulation: predator and prey move together.—The analytic solutions presented above required that we varied only the movement of the predator or the prey; they do not, therefore, address the more realistic situation in which both species move. To examine this, we used numerical simulations (as analytic solutions could not be obtained). To begin, we ignored larval connectivity. Predator movement, in the presence of prey movement, showed similar positive benefits to prey density

in the MPA as observed in the analytic solutions; that is, at low predator movement rates, the trophic cascade pattern occurred, but as predator movement increased (especially when prey movement was low), prey density often increased above what it was before creation of the MPA (Fig. 4a). However, as observed in the analytic results, this increase in prey density was not possible when fishing mortality on predators was very high (Fig. 4b). The effect of prey movement differed from our analytic results. When fishing mortality on the predator was relatively low (Fig. 4a) and predators did not move much, trophic cascades always occurred (i.e., prey always decreased after creation of the MPA). However, at higher predator movement rates, the trophic cascade pattern occurred only under high prey movement rates: As prey movement declined, prey density increased in the MPA. Thus, prey movement reinforced the trophic cascade in this situation.

Simulation: predators and larvae move.—Because prey movement had relatively minor effects, we next focused on the simultaneous effects of larval

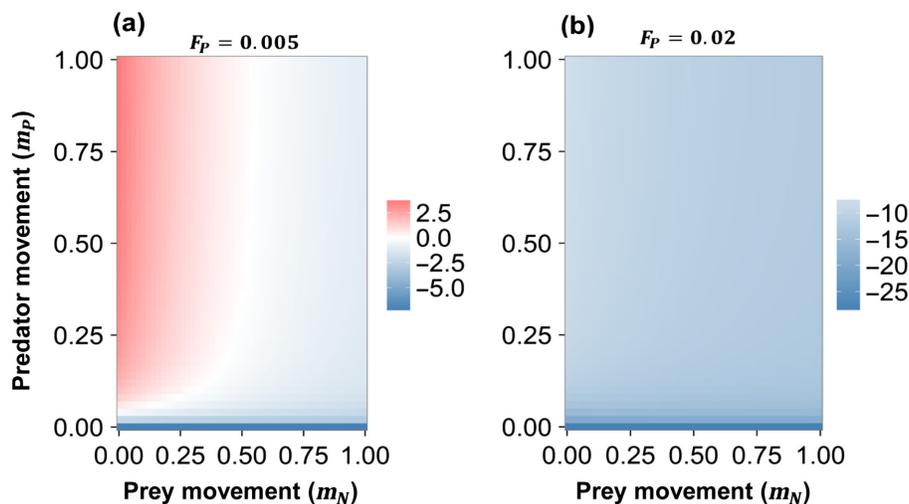


Fig. 4. Results for the specialist predator model (one-predator–one-prey model): influence of prey and predator movement rates (m_N and m_P) on the change in prey density in the marine protected area (MPA) in the absence of larval connectivity ($p = 0$) under two levels of fishing mortality on predators but with constant fishing mortality on prey ($F_N = 0.25$): (a) $F_P = 0.005/\text{yr}$; (b) $F_P = 0.02/\text{yr}$. Blue shading indicates that prey density decreased after building the MPA, whereas red indicates prey density increased. Parameters were chosen to illustrate the effect of prey movement for different baseline situations in Fig. 3d (i.e., panel a used fishing rates that correspond to parameters in which the prey response shifted from negative to positive as m_P increased [e.g., F_P and F_N fall into the red region of Fig. 3d], whereas the conditions in panel b always resulted in decreased prey density [blue region] in Fig. 3d). Other parameter values are given in Table 1.

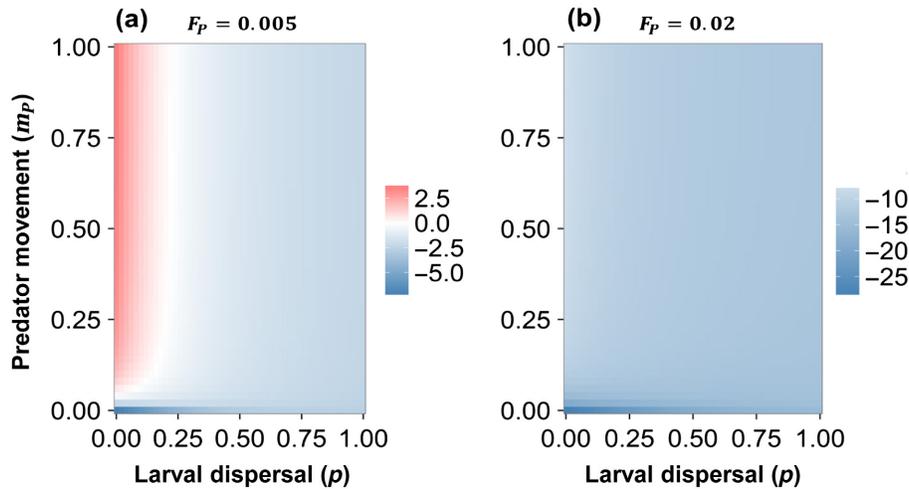


Fig. 5. Results for the specialist predator model (one-predator–one-prey model): effects of larvae dispersal (p) and the predator movement rate (m_p) on the change in prey density in the marine protected area (MPA) (when $m_N = 0$ and $F_N = 0.25$) under two levels of fishing mortality on predators: (a) $F_p = 0.005/\text{yr}$; (b) $F_p = 0.02/\text{yr}$. Colors indicate the direction of change in prey density before and after building the MPA: Increased prey density is indicated by red, whereas decreased prey density is indicated by blue. All the other parameter values are given in Table 1.

connectivity (assumed equal for predator and prey) and predator movement. These results mirrored those seen for predator and prey movement (compare Figs. 5 to 4). Briefly, when predator fishing mortality (F_p) was relatively low, increased predator movement (m_p), in combination with low larval connectivity (p), led to a reversal of the trophic cascade in the MPA (see left-hand side of Fig. 5a). Increasing larval connectivity returned the system to a trophic cascade (i.e., right-hand side of Fig. 5a). Under high levels of predator fishing mortality (F_p), the trophic cascade pattern always occurred (Fig. 5b).

Generalist predator (two-prey) model with movement

The above analyses showed that predator movement could strongly influence the effects of protection on the prey of a specialist predator and reverse the expectation of a trophic cascade. However, predators are rarely specialists, and the presence of alternative prey can alter the effects of predators on herbivores (Rizzari 2014); thus, we evaluated whether the presence of other prey altered the response of a focal prey to protection. We used the results of our previous analysis of a specialized predator model to help guide our analysis of a generalized predator feeding on

two prey species: a focal prey and an alternative prey. The one-predator–two-prey system was:

$$\begin{aligned} \dot{N}_M = & r_N[(1-p)N_M + pN_F] - eN_M^2 - \mu_N N_M \\ & - a_N N_M P_M + m_N(N_F - N_M) \end{aligned} \quad (9)$$

$$\begin{aligned} \dot{S}_M = & r_S[(1-p)S_M + pS_F] - eS_M^2 - \mu_S S_M \\ & - a_S S_M P_M + m_S(S_F - S_M) \end{aligned} \quad (10)$$

$$\begin{aligned} \dot{P}_M = & c[(1-p)(a_N N_M P_M + a_S S_M P_M) + p(a_N N_F P_F \\ & + a_S S_F P_F)] - \mu_P P_M + m_p(P_F - P_M) \end{aligned} \quad (11)$$

$$\begin{aligned} \dot{N}_F = & r_N[(1-p)N_F + pN_M] - eN_F^2 - \mu_N N_F \\ & - a_N N_F P_F - F_N N_F + m_N(N_M - N_F) \end{aligned} \quad (12)$$

$$\begin{aligned} \dot{S}_F = & r_S[(1-p)S_F + pS_M] - eS_F^2 - \mu_S S_F \\ & - a_S S_F P_F - F_S S_F + m_S(S_M - S_F) \end{aligned} \quad (13)$$

$$\begin{aligned} \dot{P}_F = & c[(1-p)(a_N N_F P_F + a_S S_F P_F) + p(a_N N_M P_M \\ & + a_S S_M P_M)] - \mu_P P_F - F_P P_F + m_p(P_M - P_F) \end{aligned} \quad (14)$$

where $F_S = qF_N$, the state variables N_M , N_F , S_M , S_F , P_M , and P_F are the densities of focal prey, alternative prey and predator in the MPA and the

fishing ground respectively, and all the other parameters are defined in Table 1. We assumed that the prey did not directly compete, but rather interacted only through the predator. Without loss of generality, we assumed that the alternative prey had the same natural and density-dependent mortality rates as focal prey. We further assumed that the predator attack rate was higher, but the fishing rate was lower, on the alternative prey (as done by Kellner et al. 2010 for their “other prey”).

We first analytically solved the equilibria of the system when only the predators moved ($m_p \geq 0$; $m_N = 0$, $m_S = 0$, and $p = 0$). We then simulated the dynamics when both the predator and alternative prey moved (i.e., in the absence of larval connectivity or movement of the focal prey). We did not reanalyze the influence of focal prey movement given the results of the specialist predator model.

Analytic approach: only predators move.—In the absence of prey movement and larval connectivity, predator movement could decrease predator density but increase focal prey density in the MPA (Eqs. 93 and 94 in Appendix S5). This trend was similar to the results obtained with the one-prey model (Eqs. 50 and 51 in Appendix S3).

Although predator density in the MPA decreased with an increase in predator movement, it remained higher than before building the MPA (Eq. 97 in Appendix S5), indicating that establishment of the MPA always benefited the predator. However, whether the MPA increased the density of the focal prey after creation of the MPA depended on the predator movement rate (m_p) as well as the fishing rates (F_N and F_p ; recall that $F_S = qF_N$; Fig. 6 and Appendix S5; Fig. S1; detailed calculations are in Appendices S4 and S5).

When predators could not move ($m_p = 0$), there were three primary regions of F_N – F_p space (Fig. 6a). At low fishing mortality rates, the alternative prey was extinct both before and after building the MPA (area A1 in Fig. 6a); thus, the result was the same as obtained for the one-prey model. At greater fishing rates (i.e., area above the black dotted line in Fig. 6a), all three species were extant before the creation of the MPA but the alternative prey went extinct after building the MPA. The focal prey decreased in density under relatively high predator fishing rates (area B1 in Fig. 6a), and reversal of the trophic cascade

happened when fishing rates were relatively low on the predator but high on the prey (area B2 in Figs. 6a and S3).

The parameter space that reversed the trophic cascade was larger for the generalist predator (Fig. 6) relative to the specialist predator (Fig. 3). This was seen most clearly when predators did not move (compare Figs. 3a and 6a); that is, region B2 in Fig. 6a does not exist in Fig. 3a. Recall, that the alternative prey went extinct in region B2 after creation of the MPA. Thus, the density of the focal prey after building the MPA was the same in both models. However, the focal prey density before the creation of the MPA was lower in the two-prey model because of the effect of apparent competition on the focal prey (Holt 1977, Kellner et al. 2010). This effect reduced the focal prey density before the creation of the MPA in the two-prey model and therefore made it easier for the focal prey density to increase following protection.

As predator movement increased (e.g., $m_p = 0.01$), more predators moved out of the MPA, which reduced predation on the focal prey and expanded the F_N – F_p space in which focal prey density increased after building the MPA (i.e., note the expansion of regions A2 and B2 and eventually C2 in Fig. 6). Simultaneously, increased predator movement further released alternative prey density and increased the area in which the three species persisted after building the MPA (i.e., areas C1, C2, and A3). The region in which the focal prey increased in density, expanded to a maximum as predator movement further increased ($m_p \rightarrow \infty$; Fig. 6d). Notice also that the two-prey system (Fig. 6) had a greater region in which the predator was extant before the creation of the MPA (relative to the one-prey system; Fig. 3), as indicated by the cross-hatched area in both Figs. 3 and 6. This further effect, combined with the effect of predator movement, further expanded the region in which an extant predator and its focal prey both increased in abundance following protection.

In summary, the presence of an alternative prey can reverse the expected trophic cascade in the MPA (area B2 in Fig. 6a). This result was previously demonstrated by Kellner et al. (2010). More significantly, an increase in predator movement also could increase focal prey density and reverse the trophic cascade pattern in the MPA site (compare

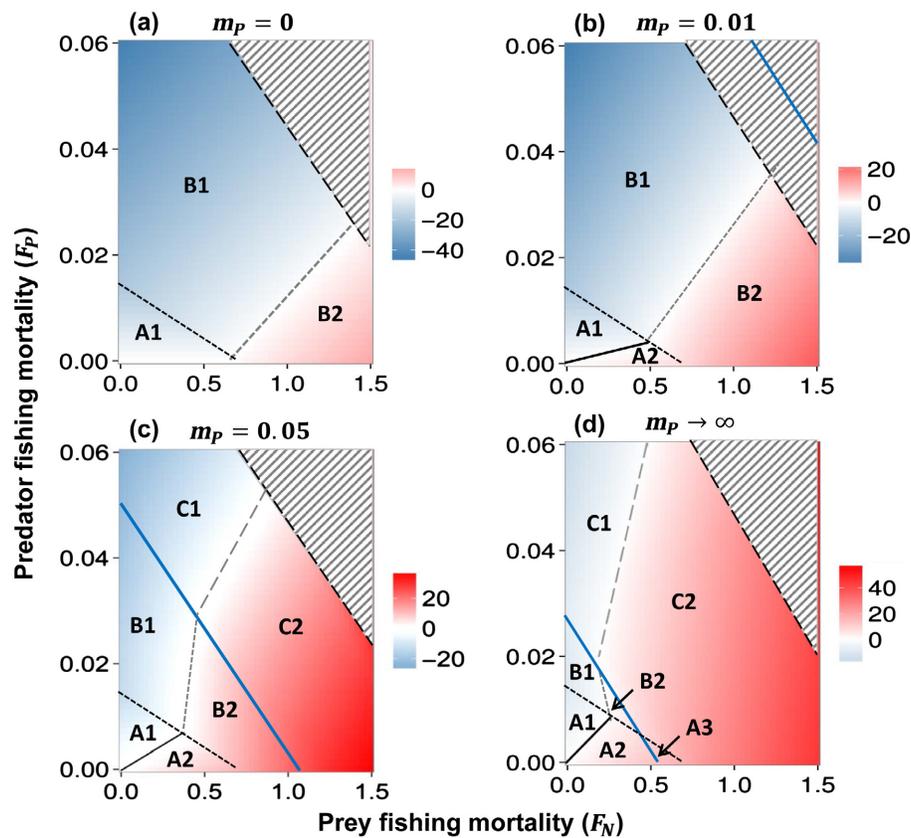


Fig. 6. Results for the generalist predator model (one-predator-two-prey model): change in focal prey density after building the marine protected area (MPA) in relation to fishing rates under four predator movement rates ($m_p = 0, 0.01, 0.05$ and ∞ /yr). At high fishing rates, predators are extinct before building the MPA. The remaining space is divided into seven regions: A1 and A2: alternative prey is always extinct (similar to the specialist predator case); A3: alternative prey is extinct before but extant after building the MPA; B1 and B2: the alternative prey goes extinct after building the MPA; and C1 and C2: all species are always extant. Focal prey density decreases in blue regions (A1, B1, and C1) but increases in red regions (A2, A3, B2, C2). As $m_p \rightarrow \infty$, B1 and B2 shrink, but C1 and C2 expand. The solid black line, the gray dotted line and the gray dashed line all converge when $m_p \rightarrow \infty$. Other parameters and detail calculations are given in Appendix S5.

Fig. 6a with d). This effect was similar to the one we observed in the one-prey model (Fig. 3).

Simulation: predator and alternative prey move.— The previous analysis demonstrated the importance of predator movement. We next simulated the effect of movement of the alternative prey as well as the predator. We started by ignoring larval connectivity (i.e., $p = 0$), fixing the fishing rate on prey ($F_N = 0.2$), and varying the fishing rate on the predator ($F_p = 0.005$ and 0.02), as in the analyses for the one-prey model (Fig. 4). At low predator fishing rates ($F_p = 0.005$), trophic cascades always occurred in the MPA

(Appendix S5: Fig. S2a). However, at a greater fishing rate ($F_p = 0.02$), predator movement, but not alternative prey movement, could reverse the expected trophic cascade (Appendix S5: Fig. S2b).

Simulations: predators and larvae move.— Next, we studied the combined effects of predator movement (m_p) and larval dispersal (p) in the absence of prey movement ($m_N = 0$ and $m_S = 0$). We assumed that larval connectivity was equal for all the three species. The result we obtained was similar to the results when only the predator and alternative prey moved (compare Appendix S5: Fig. S3 with S2).

Briefly, when predator fishing mortality (F_p) was relatively low ($F_p = 0.005$), the trophic cascade always occurred (Appendix S5: Fig. S3a), but when F_p was larger ($F_p = 0.02$), predator movement could reverse the trophic cascade (Appendix S5: Fig. S3b). Larval connectivity could increase focal prey density but it could not reverse the trophic cascade (Appendix S5: Fig. S3b).

INTERACTIONS WITH TWO FORMER MECHANISMS

Previous models (e.g., Baskett 2006, Kellner et al. 2010) examined the effects of prey size refuge (Baskett 2006) and predator density-dependent mortality (Kellner et al. 2010) in the absence of post-settlement movement of the predator (and prey). This allowed the calculation of solutions for predator density in the MPA (i.e., by setting $F_N = 0$ and $F_p = 0$) without having to simultaneously consider the effect of connectivity with the fishing grounds. However, this approach will overestimate predator density in the MPA if predators move because movement will tend to homogenize the density difference inside vs. outside the MPA (see Gerber et al. 2003, Claudet et al. 2010, Langebrake et al. 2012). To better understand the relative effects of all three possible mechanisms—predator movement (see *Generalist predator (two-prey) model with movement*), prey size refuge (Baskett 2006) and predator density-dependent mortality (Kellner et al. 2010)—we built a final model based on Eqs. 9–14 that included all three mechanisms:

$$N_{S_M} = r_N[(1-p)N_{L_M} + pN_{L_F}] - eN_{S_M}^2 - \mu_N N_{S_M} - a_{N_S} N_{S_M} P_M - \gamma N_{S_M} \quad (15)$$

$$N_{L_M} = \gamma N_{S_M} - \mu_N N_{L_M} - a_{N_L} N_{L_M} P_M \quad (16)$$

$$S_M = r_S[(1-p)S_M + pS_F] - eS_M^2 - \mu_S S_M - a_S S_M P_M \quad (17)$$

$$P_M = c[(1-p)(a_{N_S} N_{S_M} P_M + a_{N_L} N_{L_M} P_M + a_S S_M P_M) + p(a_{N_S} N_{S_F} P_F + a_{N_L} N_{L_F} P_F + a_S S_F P_F)] - \mu_P P_M - e_P P_M^2 + m_P (P_F - P_M) \quad (18)$$

$$N_{S_F} = r_N[(1-p)N_{L_F} + pN_{L_M}] - eN_{S_F}^2 - \mu_N N_{S_F} - a_{N_S} N_{S_F} P_F - \gamma N_{S_F} - F_N N_{S_F} \quad (19)$$

$$N_{L_F} = \gamma N_{S_F} - \mu_N N_{L_F} - a_{N_L} N_{L_F} P_F - F_N N_{L_F} \quad (20)$$

$$S_F = r_S[(1-p)S_F + pS_M] - eS_F^2 - \mu_S S_F - a_S S_F P_F - F_S S_F \quad (21)$$

$$P_F = c[(1-p)(a_{N_S} N_{S_F} P_F + a_{N_L} N_{L_F} P_F + a_S S_F P_F) + p(a_{N_S} N_{S_M} P_M + a_{N_L} N_{L_M} P_M + a_S S_M P_M)] - \mu_P P_F - e_P P_F^2 - F_P P_F + m_P (P_M - P_F) \quad (22)$$

where focal prey (N_M and N_F) in the former models are now subdivided into two size classes (small juveniles, and large adults denoted by additional subscripts S and L). A size refuge (the large size were less invulnerable to predation) is indicated by reductions in a_{N_L} (when $a_{N_L} = 0$, large adults totally escape predation). We assumed that small and large classes were fished equally (F_N is the fishing rate) and had the same natural mortality rate (μ_N). Predators incurred direct density-dependent mortality (e_p), the absence of which was indicated by $e_p = 0$. All other aspects of the model (and meanings of variables) were as presented previously.

We examined the change in focal prey density (small plus large sizes) before and after building the MPA. We chose equal fishing rates on prey and predator ($F_N = F_p$) based on a recent synthesis (Darimont et al. 2015). To evaluate the role of the three mechanisms, we separately varied the attack rate on large prey (a_{N_L}) and the strength of predator density-dependent mortality (e_p) under three predator movement rates and across a range of fishing rates (in which $F_N = F_p$). Finally, we checked whether these qualitative results were consistent under a different fishing rate combination (i.e., when $F_N = 5F_p$; results in Appendix S6).

In the absence of predator movement, neither a prey size refuge (decreasing a_{N_L}) nor predator density-dependent mortality (increasing e_p) could reverse the trophic cascade (Fig. 7a, d). However, as predator movement (m_p) increased, the parameter space in which the trophic cascade was reversed increased (Fig. 7b, c, e, f). Movement reinforced these other two mechanisms: In the presence of predator movement, reducing the predation rate on large prey (a_{N_L}) or increasing predator density-dependent mortality (e_p)

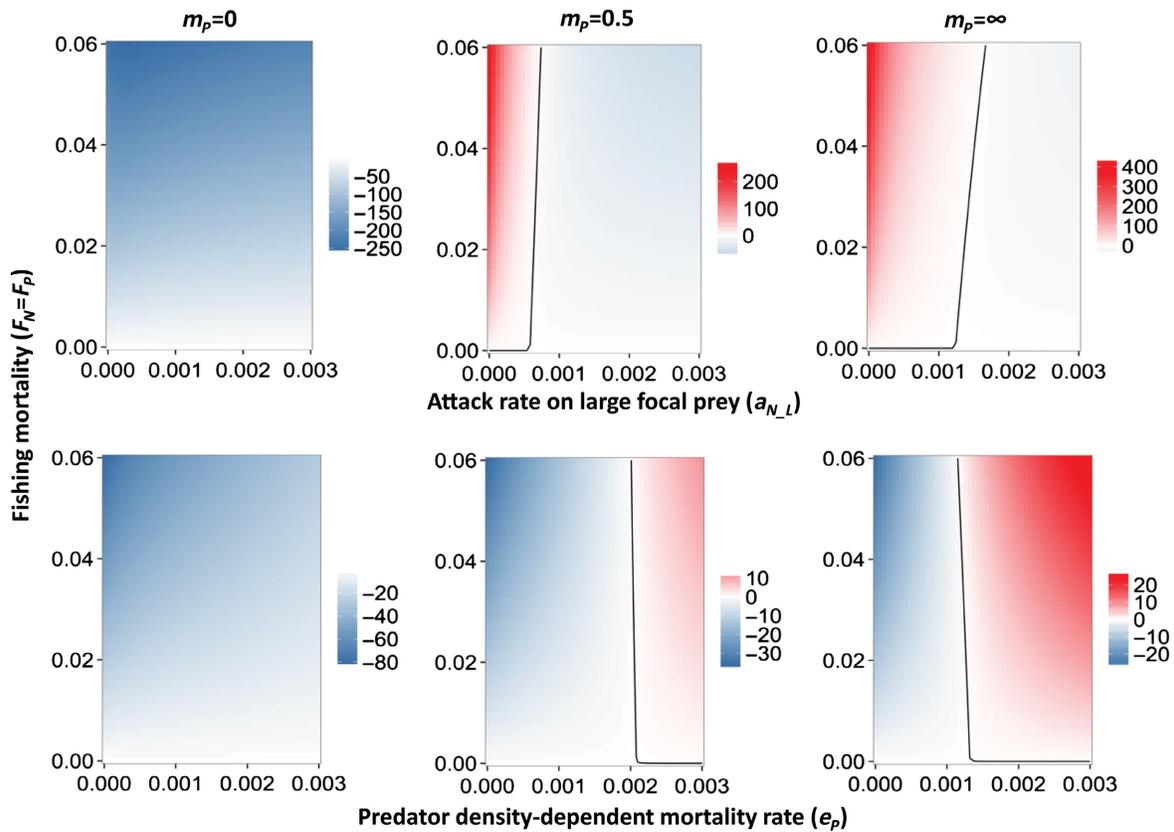


Fig. 7. Results for the full model (one-predator–two-prey model with two size focal prey classes) under all three mechanisms (focal prey size refuge, predator density-dependent mortality and predator movement): change in the density of focal prey ($N_S + N_L$) from before to after the creation of marine protected areas (MPAs) in relation to fishing mortality rate and either the magnitude of the prey size refuge for the large prey (panels a, b, c) or changes in the predator’s density-dependent mortality (panels d, e, f) for three predator movement rates ($m_p = 0, 0.05$ and ∞). In all cases, fishing rates on prey and predator are equal to each other ($F_N = F_P$). Colors indicate the direction of change in focal prey density after building the MPA: Blue indicates decreased prey density, whereas red indicates increased prey density. Black lines, which separate the above two, show parameter combinations that yield no change in focal prey density from before to after building the MPA. Other parameter values are given in Table 1.

caused prey density to change from decreasing (i.e., a trophic cascade; see “blue” regions in Fig. 7) to increasing (the “red” regions). This effect was similar under other fishing rate combinations (e.g., $F_N = 5F_P$; Appendix S6: Fig. S1b, c, e, f), except that prey size refuge and predator density-dependent mortality could reverse trophic cascades by themselves (e.g., $F_N = 5F_P$ in Appendix S6: Fig. S1a, d). This latter result (when fishing is greater on prey than predators) is consistent with earlier studies (Baskett 2006, Kellner et al. 2010).

DISCUSSION

Our study, demonstrates that one seemingly intuitive mechanism for the absence of trophic cascades in the MPA—the reduction of fishing on prey as well as predator—is necessary, but not sufficient (Fig. 1a), to explain the increased density of predators and prey that have been observed in some MPA systems (Mumby et al. 2006). Instead, we show that other mechanisms are required (see also Baskett 2006 and Kellner et al. 2010). In particular, we show that predator

movement, in combination with reduced prey mortality, can lead to increased prey density inside of MPAs. Indeed, many spatially explicit individual based models (e.g., deRoos et al. 1991, Mccauley et al. 1996, Cuddington and Yodzis 2002) have shown that movement can greatly alter the outcome of species interactions in multi-patch systems. Our study, using both analytic and numeric methods, adds to this body of literature. Of course, our study only explored the effects of random movement, yet other more complex possibilities exist (e.g., Fryxell et al. 2008, and see Langebrake et al. 2012 for an example with MPAs). Despite these potential complexities, the actual movement of predators and prey can often be approximated using only random movement models (e.g., incorporating Lévy flights; Sims et al. 2008); thus, we suspect that our results are likely to provide general insight about the response of these systems to protection.

Phenomenologically, the mechanisms can be envisioned in a common framework, in which a predator's isocline "slants to the right" (Fig. 1b; Mittelbach et al. 1988). The source of the "slant" comes from a reduction in the per capita growth rate of the predator (e.g., due to a lower attack rate) as predator density increases. This reduction could be caused by the following: interference or other forms of direct density dependence (e.g., territoriality or cannibalism or ratio dependence) among the predators (see Mittelbach et al. 1988, Arditi and Ginzburg 1989, Kellner et al. 2010); a prey size refuge from predation that dilutes the actual prey density (see Chase 1999, Baskett 2006, Mumby et al. 2006); prey spatial structure (Mittelbach et al. 1988); or a generalist predator that is also limited by another resource (Kellner et al. 2010). Our study further shows that predator movement reduces predator density in the MPA, which effectively reduces predator encounters with their prey (see also Barraquand and Murrell 2013).

As predator movement increases, predator density decreases, but focal prey density increases in the MPA (Eqs. 50 and 51 in Appendix S3, and Eqs. 93 and 94 in Appendix S5). Although this can lead to a reversal of the trophic cascade (e.g., as in Fig. 1b), it is not always the case (e.g., the blue regions in Figs. 3 and 6). Trophic cascades typically result when there is relatively high fishing on the predator (e.g., Figs. 3 and 6). In these cases predator density increases so much

following protection that the cascade cannot be reversed—the numerical increase in the predator population is too great and the prey density decreases.

In contrast to predator movement, prey movement or larval connectivity have relatively little effect on reversing the expected trophic cascades. These results appear to be robust, being observed in both the specialist (one-prey) and generalist (two-prey) predator models. It is somewhat surprising that larval dispersal did not have similar effects as predator movement, but we allowed larval dispersal to occur in both the predator and prey. We suspect that predator larval dispersal benefits prey in the MPA, but that prey larval dispersal has negative or no influence on focal prey density in the MPA. As a result, when larvae of all species can disperse (as they did in our simulations), the combined effects of larval dispersal tend to counteract each other and will show either negative (Fig. 5a) or reduced positive effects on focal prey density in the MPA (Appendix S5: Fig. S3b). Had we modeled larval dispersal separately for each species, we suspect that the results would have mirrored the results for post-settlement movement (e.g., as in Fig. 4 and Appendix S5: Fig. S2).

In marine systems, large carnivores (predators) likely move more than their prey (Sale et al. 2005, Grüss et al. 2011) and likely also have greater dispersal distances (Stier et al. 2014). Therefore, the high movement rate of predators likely contributes to the absence of trophic cascades in many MPA studies. This is not to say that other mechanisms do not operate. In fact, it is likely that prey size refuge (Baskett 2006) and predator density-dependent mortality (Kellner et al. 2010) also contribute, although in our simulations, those mechanisms cannot reverse the trophic cascade unless $F_N > F_P$ (compare Fig. 7 and Appendix S6: Fig. S1). Interestingly, a recent synthesis found that fishing losses did not differ across trophic levels (i.e., $F_N = F_P$, Darimont et al. 2015) suggesting those mechanisms alone cannot reverse the trophic cascade. We found that predator post-settlement movement has strong effects on its own (Figs. 3–6) and can also reinforce the other two mechanisms (Fig. 7). Unfortunately, we lack detailed empirical studies to evaluate the relative importance of these mechanisms, let alone their combined effects on dynamics of MPA systems.

In conclusion, our study shows that predator movement and the reduction of fishing on prey could increase both predator and focal prey densities in the MPA and therefore preclude the expected occurrence of trophic cascades inside MPAs. As a result, our study offers an additional explanation for the observed positive increases in both predators and prey following the establishment of MPAs. This work further highlights the importance of movement and connectivity, an issue that has received considerable attention in both marine and terrestrial ecosystems (e.g., Diffendorfer et al. 1995, Walters 2000, Loreau et al. 2003, Cowen and Sponaugle 2009, White and Samhuri 2011, Jeltsch et al. 2013, Bauer and Hoye 2014).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1421/supinfo>

Jing Jiao, Sergei S. Pilyugin and Craig W. Osenberg. Random movement of predators can eliminate trophic cascades in marine protected areas. Ecosphere

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APPENDIX S1: CHANGE IN PREDATOR AND PREY DENSITIES AFTER CREATION OF AN MPA WITHOUT MOVEMENT IN SPECIALIST PREDATOR (ONE-PREY) MODEL

In the absence of the MPA, the system is:

$$\frac{dN}{dt} = r_N N - eN^2 - \mu_N N - a_N NP - F_N N \quad (15)$$

$$\frac{dP}{dt} = ca_N NP - \mu_P P - F_P P, \quad (16)$$

which has the solution:

$$N_0^* = \frac{\mu_P + F_P}{ca_N} \quad (17)$$

$$P_0^* = \frac{ca_N(r_N - \mu_N) - ca_N F_N - e(\mu_P + F_P)}{ca_N^2} \quad (18)$$

By setting eqn. (18) = 0, we get:

$$F_P = -\frac{ca_N}{e} F_N + \frac{ca_N r_N}{e} - \frac{ca_N}{e} \mu_N - \mu_P \quad (19)$$

which separates the parameter space into a region in which the predator is extant and one in which the predator is extinct before the building of the MPA.

If predators are extinct ($P = 0$), then the prey density (solving eqn. (15) given $P = 0$) becomes:

$$N_{0,P=0}^* = \frac{r_N - \mu_N - F_N}{e} \quad (20)$$

and by setting this to 0, we can find the threshold fishing mortality that also drives the prey to extinction (conditional on the predator being extinct):

$$F_N = r_N - \mu_N \quad (21)$$

After the MPA is built, but in the absence of movement, the above analysis still applies to the fishing ground. The portion of the system in the MPA is described by setting the fishing mortality terms to 0 and solving eqns. (15) and (16):

$$N_M^* = \frac{\mu_P}{ca_N} \quad (22)$$

$$P_M^* = \frac{ca_N(r_N - \mu_N) - e\mu_P}{ca_N^2} \quad (23)$$

We assume that N_M^* and P_M^* are both positive in the MPA.

By comparing the densities after building the MPA with those before building the MPA, we can determine the conditions under which trophic cascades will or will not occur. There are three scenarios (Fig. S1).

1. If both the predator and prey have positive densities before the MPA is built (i.e., $F_P < -\frac{ca_N}{e} F_N + \frac{ca_N r_N}{e} - \frac{ca_N}{e} \mu_N - \mu_P$), then predator density increases but prey density decreases after building the MPA: i.e., compare eqns. (22), (23) with eqns. (17) and (18). In this case, trophic cascades always occur.
2. If both the predator and prey are extinct before the MPA is built (when $F_N \geq r_N - \mu_N$), then the MPA will always increase predator and prey densities. In this case, a traditional trophic cascade does not occur, but we consider this result trivial, as it requires that both the predator and prey be regionally extinct prior to building the MPA.
3. If predators are extinct but prey have a positive density before the MPA is built (i.e., when $F_P > -\frac{ca_N}{e} F_N + \frac{ca_N r_N}{e} - \frac{ca_N}{e} \mu_N - \mu_P$ and $F_N < r_N - \mu_N$), the MPA always increases predator density (i.e., from 0 to eqn. (23)). The change in prey density can be found by comparing eqns. (20) and (22). Prey density either:

- 1.increases (dark red area in Fig. S1), if $F_N > r_N - \mu_N - \frac{e \mu_P}{ca_N}$ (24)

- 2.or decreases (blue area above the dashed line in Fig. S1) if $F_N < r_N - \mu_N - \frac{e \mu_P}{ca_N}$ (25)

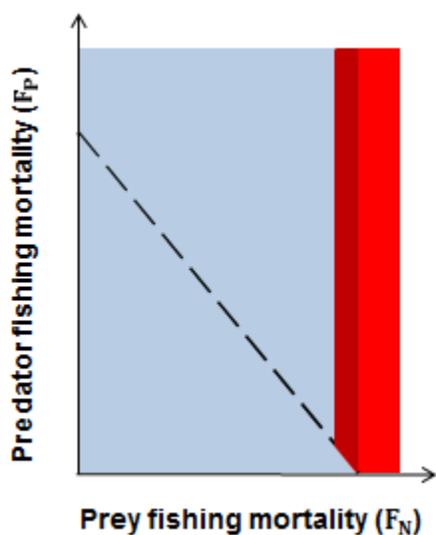


Fig. S1 Responses of predator and prey densities to MPA establishment under different fishing rates in the absence of movement. Before building the MPA, there are three density situations: 1) in the blue area under the dashed line ($F_P < -\frac{ca_N}{e} F_N + \frac{ca_N r_N}{e} - \frac{ca_N}{e} \mu_N - \mu_P$), both predator and prey have positive densities; 2) in the blue and dark red areas above the dashed line (i.e., $F_P > -\frac{ca_N}{e} F_N + \frac{ca_N r_N}{e} - \frac{ca_N}{e} \mu_N - \mu_P$ and $F_N < r_N - \mu_N$), the

predator is extinct but the prey is extant; and 3) in the lighter red area (i.e., $F_N > r_N - \mu_N$), the predator and prey are both extinct. After building the MPA, there are two qualitatively distinct responses: 1) in the blue areas predator density increases but prey density decreases (i.e., there is a trophic cascade); and 2) in the red areas, both predator and prey densities increase. Note,

however, that this increase in the predator and prey only occurs in parameter regions in which the predator and/or prey are initially extinct. Detailed calculations are in Appendix S1.

APPENDIX S2: ANALYSIS OF EFFECTS OF PREY MOVEMENT IN THE SPECIALIST PREDATOR*(ONE-PREY) MODEL*

Here, we evaluate the two-patch model with two trophic levels—predator and prey (eqns. (5)-(8))—when larvae do not move ($p = 0$) but post-settlement fish can potentially migrate between the two patches (i.e., the MPA and fishing grounds). When prey move but predators do not ($m_P = 0$), the model becomes:

$$\dot{N}_M = r_N N_M - e N_M^2 - \mu_N N_M - a_N N_M P_M + m_N (N_F - N_M) \quad (26)$$

$$\dot{P}_M = c a_N N_M P_M - \mu_P P_M \quad (27)$$

$$\dot{N}_F = r_N N_F - e N_F^2 - \mu_N N_F - a_N N_F P_F + m_N (N_M - N_F) - F_N N_F \quad (28)$$

$$\dot{P}_F = c a_N N_F P_F - \mu_P P_F - F_P P_F \quad (29)$$

At equilibrium, eqn. (26)-(29) has a unique positive solution:

$$N_M^* = \frac{\mu_P}{c a_N} \quad (30)$$

$$P_M^* = \frac{r_N N_M^* - e N_M^{*2} - \mu_N N_M^* + m_N (N_F^* - N_M^*)}{a_N N_M^*} \quad (31)$$

$$N_F^* = \frac{\mu_P + F_P}{c a_N} \quad (32)$$

$$P_F^* = \frac{r_N N_F^* - e N_F^{*2} - \mu_N N_F^* + m_N (N_M^* - N_F^*) - F_N N_F^*}{a_N N_F^*} \quad (33)$$

The Jacobian matrix of eqn. (26)-(29) at equilibrium is:

$$J_1 = \begin{bmatrix} -\frac{m_N N_F^*}{N_M^*} - e N_M^* & -a_N N_M^* & m_N & 0 \\ c a_N P_M^* & 0 & 0 & 0 \\ m_N & 0 & -\frac{m_N N_M^*}{N_F^*} - e N_F^* & -a_N N_F^* \\ 0 & 0 & c a_N P_M^* & 0 \end{bmatrix}$$

Because all eigenvalues of J_1 are negative, this equilibrium is stable (based on Routh-Hurwitz criteria).

Using eqns. (30)-(31), we can evaluate how the equilibrium densities of prey and predators in the MPA change in response to a change in the movement rate of the prey:

$$\frac{\partial N_M^*}{\partial m_N} = 0 \quad (34)$$

$$\frac{\partial P_M^*}{\partial m_N} = N_F^* - N_M^* = \frac{F_P}{c a_N} > 0 \quad (35)$$

From eqns. (34) and (35), we see that without larvae connectivity and predator movement, the prey equilibrium density (N_M^*) does not change but the predator equilibrium

density (P_M^*) increases as prey movement rate (m_N) increases. This arises because predation in the MPA produces a sink for prey. With the increase of prey movement, more prey move into the MPA and are consumed by the enhanced predator. This increased flux of prey into the MPA drives up the predator density. Eventually at $\max(m_N)$, all prey in the system are consumed by predators, the prey go regionally extinct and the predator follows. This threshold can be found by setting $P_F^* = 0$ in eqn. (33):

$$\max(m_N) = \frac{(\mu_P + F_P)[c a_N (r_N - \mu_N - F_N) - e(\mu_P + F_P)]}{c a_N F_P} \quad (36)$$

APPENDIX S3: ANALYSIS OF EFFECTS OF PREDATOR MOVEMENT IN THE SPECIALIST PREDATOR (ONE-PREY) MODEL

Here, we take a similar approach as in Appendix S2, but instead of analyzing the effects of prey movement, we focus on the effects of predator movement (i.e., $m_N = 0$):

$$\dot{N}_M = r_N N_M - e N_M^2 - \mu_N N_M - a_N N_M P_M \quad (37)$$

$$\dot{P}_M = ca_N N_M P_M - \mu_P P_M + m_P (P_F - P_M) \quad (38)$$

$$\dot{N}_F = r_N N_F - e N_F^2 - \mu_N N_F - a_N N_F P_F - F_N N_F \quad (39)$$

$$\dot{P}_F = ca_N N_F P_F - \mu_P P_F - F_P P_F + m_P (P_M - P_F) \quad (40)$$

The Jacobian matrix J_2 of eqns. (37)-(40) is:

$$J_2 = \begin{bmatrix} -eN_M^* & -aN_M^* & 0 & 0 \\ caP_M^* & -\frac{m_P P_F^*}{P_M^*} & 0 & m_P \\ 0 & 0 & -eN_F^* & -aN_F^* \\ 0 & m_P & caP_F^* & -\frac{m_P P_F^*}{P_M^*} \end{bmatrix}$$

J_2 fits Routh-Hurwitz criteria for a 4 by 4 matrix, so J_2 has negative eigenvalues. Thus, the equilibrium is stable. Next, we prove the uniqueness of this solution. For computational convenience, we let $\rho = \frac{P_M^*}{P_F^*}$, set equations (37)-(40) to 0, and solve for the four equilibria:

$$N_M^* = \frac{1}{ca_N} [\mu_P + m_P (1 - \frac{1}{\rho})] \quad (41)$$

$$P_M^* = \frac{1}{a_N} [r_N - \mu_N - eN_M^*] \quad (42)$$

$$N_F^* = \frac{1}{ca_N} [\mu_P + F_P + m_P(1 - \rho)] \quad (43)$$

$$P_F^* = \frac{1}{a_N} [r_N - eN_F^* - \mu_N - F_N] \quad (44)$$

If we assume that all these equilibria are positive in the absence of movement ($m_P = 0$), we get the condition by setting eqns. (41)-(44) larger than 0:

$$\frac{r_N}{e} - (\frac{\mu_N}{e} + \frac{1}{ca_N} \mu_P) > 0 \text{ and } \frac{r_N}{e} - (\frac{\mu_N}{e} + \frac{1}{ca_N} \mu_P) - \frac{1}{ca_N} F_P - (\frac{1}{e}) F_N > 0.$$

Then, we substitute (41) into (42) and (43) into (44), and take the ratio of the two, we obtain:

$$\frac{P_M^*}{P_F^*} = \rho = \frac{\frac{r_N}{e} - (\frac{\mu_N}{e} + \frac{1}{ca_N} \mu_P) - \frac{1}{ca_N} m_P (1 - \frac{1}{\rho})}{\frac{r_N}{e} - (\frac{\mu_N}{e} + \frac{1}{ca_N} \mu_P) - \frac{1}{ca_N} F_P - (\frac{1}{e}) F_N + \frac{1}{ca_N} m_P (\rho - 1)} = \frac{\frac{r_N}{e} - \mu' - m'_P (1 - \frac{1}{\rho})}{\frac{r_N}{e} - \mu' - F'_P - (\frac{r_N}{e}) F'_N + m'_P (\rho - 1)} \quad (45)$$

where $\mu' = \frac{\mu_N}{e} + \frac{1}{ca_N} \mu_P$, $m'_P = \frac{1}{ca_N} m_P$, $F'_P = \frac{1}{ca_N} F_P$ and $F'_N = \frac{F_N}{r_N}$.

Eqn. (45) can be transformed as a function of ρ and m'_p (we use G as the notation for this function) for further computational convenience:

$$G(\rho, m'_p) := m'_p \rho (\rho - 1) + \left(\frac{r_N}{e} - \mu' - F'_P - \frac{r_N}{e} F'_N \right) \rho + m'_p \left(1 - \frac{1}{\rho} \right) - \left(\frac{r_N}{e} - \mu' \right) = 0 \quad (46)$$

To fit eqn. (46), ρ must be in $(1, +\infty)$ because if $0 < \rho \leq 1$, $G(\rho, m'_p) < 0$.

$$\text{From eqn. (46), we get: } \frac{\partial G}{\partial \rho} = m'_p (2\rho - 1) + \frac{r_N}{e} - \mu' - F'_P - \frac{r_N}{e} F'_N + m'_p \frac{1}{\rho^2} > 0$$

$$\text{and } \frac{\partial G}{\partial m'_p} = \rho(\rho - 1) + 1 - \frac{1}{\rho} = (\rho - 1) \left(\rho + \frac{1}{\rho} \right) > 0$$

Using implicit differentiation, we conclude that

$$\frac{\partial \rho}{\partial m'_p} = - \frac{\frac{\partial G}{\partial m'_p}}{\frac{\partial G}{\partial \rho}} < 0 \quad (47)$$

So the root $\rho = \rho(m'_p)$ is unique and it is monotonically decreasing with the increase of m'_p . A few more steps are needed to seek the relationship between N_M^* (and P_M^*) and m'_p instead of ρ and m'_p :

From $G(\rho, m'_p) = 0$, we have:

$$m'_p \left(1 - \frac{1}{\rho} \right) = \frac{\frac{r_N}{e} - \mu' - \rho \left(\frac{r_N}{e} - \mu' - F'_P - \frac{r_N}{e} F'_N \right)}{\rho^2 + 1} \quad (48)$$

Because $\rho > 1$, eqn. (48) > 0 , then we have $\frac{r_N}{e} - \mu' - \rho \left(\frac{r_N}{e} - \mu' - F'_P - \frac{r_N}{e} F'_N \right) > 0$, which leads to:

$$\frac{\partial [m'_p (1 - \frac{1}{\rho})]}{\partial \rho} = \frac{- \left(\frac{r_N}{e} - \mu' - F'_P - \frac{r_N}{e} F'_N \right) (\rho^2 + 1) - \left[\frac{r_N}{e} - \mu' - \rho \left(\frac{r_N}{e} - \mu' - F'_P - \frac{r_N}{e} F'_N \right) \right] 2\rho}{(\rho^2 + 1)^2} < 0 \quad (49)$$

Therefore, from eqn. (41)-(42), we have:

$$\frac{\partial N_M^*}{\partial \rho} = \frac{\partial \left[\frac{1}{c_{aN}} [\mu_P + m_P \left(1 - \frac{1}{\rho} \right)] \right]}{\partial \rho} \propto \frac{\partial [m'_p (1 - \frac{1}{\rho})]}{\partial \rho} < 0$$

$$\frac{\partial P_M^*}{\partial \rho} \propto - \frac{\partial N_M^*}{\partial \rho} > 0$$

Then, based on eqn. (47), we get:

$$\frac{\partial N_M^*}{\partial m'_p} > 0 \quad (50)$$

$$\frac{\partial P_M^*}{\partial m'_p} < 0 \quad (51)$$

Next, we will determine if the increase of m'_p can cause the prey's equilibrium density in the MPA (N_M^*) to exceed its density before building the MPA (N_0^*). Because N_M^* approaches its maximum as $m_p \rightarrow \infty$, a necessary condition for $N_M^* > N_0^*$ is that $\lim_{m_p \rightarrow \infty} N_M^* > N_0^*$. The similar condition for the predator is: $\lim_{m_p \rightarrow \infty} P_M^* > P_0^*$.

Using eqn. (48) and evaluating its limit as $m_P \rightarrow \infty$ (same as $\rho \rightarrow 1$), we obtain:

$$\lim_{m_P \rightarrow \infty} m'_P \left(1 - \frac{1}{\rho}\right) = \lim_{m_P \rightarrow \infty} \frac{\frac{r_N - \mu' - \rho}{e} \left(\frac{r_N - \mu' - F'_P - \frac{r_N F'_N}{e}}{\rho^2 + 1}\right) \rightarrow \frac{F'_P + \frac{r_N F'_N}{e}}{2}}{2}.$$

$$\begin{aligned} \text{Therefore, } \lim_{m_P \rightarrow \infty} N_M^* &\rightarrow \lim_{m_P \rightarrow \infty} \frac{1}{ca_N} \left[\mu_P + ca_N m'_P \left(1 - \frac{1}{\rho}\right) \right] = \frac{1}{ca_N} \left[\mu_P + ca_N \frac{F'_P + \frac{r_N F'_N}{e}}{2} \right] = \\ &\frac{1}{ca_N} \left[\mu_P + \frac{F_P}{2} + \frac{ca_N}{2e} F_N \right] \end{aligned} \quad (52)$$

$$\lim_{m_P \rightarrow \infty} P_M^* = \lim_{m_P \rightarrow \infty} \frac{1}{a} [r_N - \mu_N - eN_M^*(m_P)] = \frac{1}{a} \left\{ r_N - \mu_N - \frac{e}{ca_N} \left[\mu_P + \frac{F_P}{2} + \frac{ca_N}{2e} F_N \right] \right\} \quad (53)$$

When both predator and prey densities are positive before the MPA is built (N_0^* and P_0^* are from eqns. (3)-(4) with $b = 1$), we have:

$$\lim_{m_P \rightarrow \infty} N_M^* - N_0^* = \frac{1}{2e} F_N - \frac{1}{2ca_N} F_P = \frac{1}{2} \left(\frac{F_N}{e} - \frac{F_P}{ca_N} \right) \quad (54)$$

$$\lim_{m_P \rightarrow \infty} P_M^* - P_0^* = \frac{1}{2} \left(\frac{F_N}{a} + \frac{eF_P}{ca_N^2} \right) \quad (55)$$

Thus, the predator density always increases in the MPA (eqn. (55)). The prey increase in the MPA when:

$$\frac{F_P}{F_N} < \frac{ca_N}{e} \quad (56)$$

This solution corresponds to the red area in Fig. A4.

If, instead, $\frac{F_P}{F_N} > \frac{ca_N}{e}$, then predator density increases but prey density decreases in the MPA. Thus, a trophic cascade results (as indicated by the blue area below the dashed line in Fig. S1).

If predators are regionally extinct (area above the dashed line in Fig. S2), but prey are extant prior to building the MPA (N_0^* is from eqn. (20) in Appendix S1), predator density still increases after building the MPA, but we have a different result for the prey:

$$\lim_{m_P \rightarrow \infty} N_M^* - N_0^* = \frac{1}{ca_N} \left[\mu_P + \frac{F_P}{2} + \frac{ca_N}{2e} F_N \right] - \frac{r_N - \mu_N - F_N}{e} = \frac{1}{ca_N} \mu_P - \frac{r_N}{e} + \frac{\mu_N}{e} + \frac{3F_N}{2e} + \frac{F_P}{2ca_N} \quad (57)$$

If prey density increases after building the MPA (eqn. (57) > 0 ; red striped area in Fig. S1), we have the condition:

$$F_P > \frac{2ca_N r_N - 2ca_N \mu_N - 2e\mu_P - 3ca_N F_N}{e} \quad (58)$$

If eqn. (58) cannot be held, trophic cascade will happen (blue area above the dashed line in Fig. S1).

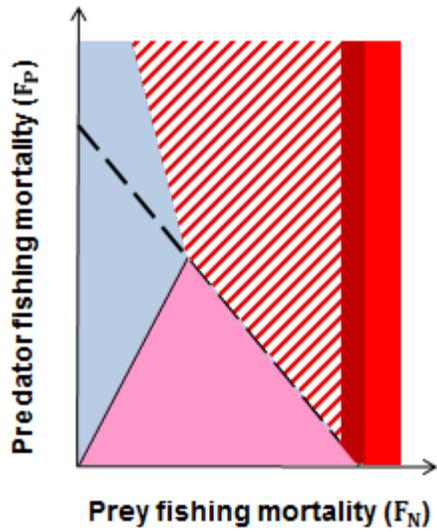


Fig. S1 Responses of predator and prey densities to MPA establishment under different fishing rates when predator movement tends to infinite. Before building the MPA, there are three density situations: 1) under the dashed line ($F_P < -\frac{ca_N}{e} F_N + \frac{ca_N r_N}{e} - \frac{ca}{e} \mu_N - \mu_P$), both predator and prey have positive densities; 2) in the blue area above the dashed line, the red striped area and dark red area ($F_P > -\frac{ca_N}{e} F_N + \frac{ca_N r_N}{e} - \frac{ca_N}{e} \mu_N - \mu_P$ and $F_N < r_N - \mu_N$), the

predator is extinct but the prey is extant; 3) in the red area ($F_N > r_N - \mu_N$), both species are

extinct. After building the MPA, densities can change in three ways: 1) in the blue area

($\frac{ca_N}{e} F_N < F_P < \frac{2ca_N r_N - 2ca_N \mu_N - 2e\mu_P - 3ca_N F_N}{e}$), predator density increases while prey density

decreases after building the MPA (trophic cascade); in the pink area below the dashed line ($F_P <$

$-\frac{ca_N}{e} F_N + \frac{ca_N r_N}{e} - \frac{ca_N}{e} \mu_N - \mu_P$ and $\frac{F_P}{F_N} < \frac{ca_N}{e}$) and in the red striped area

($\frac{2ca_N r_N - 2ca_N \mu_N - 2e\mu_P - 3ca_N F_N}{e} < F_P < r_N - \mu_N - \frac{e\mu_P}{ca_N}$), predator and prey densities both increase

after building the MPA; in the dark red and red area ($F_P > r_N - \mu_N - \frac{e\mu_P}{ca_N}$), the predator and

prey both increase their densities. Detailed calculations are in Appendix S1 and S3.

**APPENDIX S4: CHANGE IN PREDATOR AND PREY DENSITIES AFTER CREATION OF AN MPA WITHOUT
MOVEMENT IN THE GENERALIST PREDATOR (TWO-PREY) MODEL**

Before building the MPA, eqns. (12)-(14) become:

$$\dot{N} = r_N N - eN^2 - \mu_N N - a_N NP - F_N N \quad (59)$$

$$\dot{S} = r_S S - eS^2 - \mu_S S - a_S SP - F_S S \quad (60)$$

$$\dot{P} = c(a_N NP + a_S SP) - \mu_P P - F_P P \quad (61)$$

where $F_S = qF_N$ (qF_N is used in the following).

The solutions at equilibrium are:

$$S_0^* = \frac{a_N^2(r_S - \mu_S - qF_N) - a_S a_N(r_N - \mu_N - F_N) + \frac{e}{c} a_S(\mu_P + F_P)}{e(a_S^2 + a_N^2)} \quad (62)$$

$$N_0^* = \frac{a_S^2(r_N - \mu_N - F_N) - a_S a_N(r_S - \mu_S - qF_N) + \frac{e}{c} a_N(\mu_P + F_P)}{e(a_S^2 + a_N^2)} \quad (63)$$

$$P_0^* = \frac{a_N(r_N - \mu_N - F_N) + a_S(r_S - \mu_S - qF_N) - \frac{e}{c}(\mu_P + F_P)}{a_S^2 + a_N^2} \quad (64)$$

If we let $P_0^* = 0$, we can get the fishing mortality combinations where predator is extinct (area E1 and E2 in Fig. S1).

$$F_P = -\frac{c(a_S q + a_N)}{e} F_N + \frac{c a_N(r_N - \mu_N)}{e} + \frac{c a_S(r_S - \mu_S)}{e} - \mu_P \quad (65)$$

Compared to eqn. (19), this black dashed line in Appendix S5: Fig. S2 moves upper and becomes steeper compared to Fig. S1 because there is other food resource—alternative prey for predator to persist beside of focal prey.

Based on the parameters in Table 1, predators attack alternative prey S stronger than on focal prey N, so there could be fishing rates combinations where alternative prey S is extinct before building the MPA (area A1 in Fig. S1). This condition can be gotten by setting eqn. (62) = 0 (black dotted line in Fig. S3):

$$F_P = \frac{-c a_N(a_S - a_N q)}{e a_S} F_N + \frac{c a_N}{e} (r_N - \mu_N) - \frac{c a_N^2(r_S - \mu_S)}{e a_S} - \mu_P \quad (66)$$

At all the fishing rates combinations between the lines eqn. (65) and (66) (area B1 and B2 in Fig. S1), predator, focal prey and alternative prey are extant before building the MPA with their “before” densities as eqns. (62)-(64).

After building the MPA, the equilibrium densities of focal prey, alternative prey and predator become:

$$S_M^* = \frac{a_N^2(r_S - \mu_S) - a_S a_N(r_N - \mu_N) + \frac{e}{c} a_S \mu_P}{e(a_S^2 + a_N^2)} \quad (67)$$

$$N_M^* = \frac{a_S^2(r_N - \mu_N) - a_S a_N(r_S - \mu_S) + \frac{e}{c} a_N \mu_P}{e(a_S^2 + a_N^2)} \quad (68)$$

$$P_M^* = \frac{a_N(r_N - \mu_N) + a_S(r_S - \mu_S) - \frac{e}{c} \mu_P}{a_S^2 + a_N^2} \quad (69)$$

Through comparing eqns. (67)-(69) with eqns. (62)-(64), we can get the densities changes of focal prey, alternative prey and predator after building the MPA.

$$S_M^* - S_0^* = \frac{a_N^2 q F_N - a_S a_N F_N - \frac{e}{c} a_S F_P}{e(a_S^2 + a_N^2)} < 0 \quad (70)$$

$$N_M^* - N_0^* = \frac{a_N^2 F_N - a_S a_N q F_N - \frac{e}{c} a_N F_P}{e(a_S^2 + a_N^2)} \quad (71)$$

$$P_M^* - P_0^* = \frac{a_N F_N + a_S q F_N + \frac{e}{c} F_P}{a_S^2 + a_N^2} > 0 \quad (72)$$

Predator density always increases after building the MPA (eqn. (72)), alternative prey density always decreases with $a_S > a_N$ and $q = 0.5$ (eqn. (70)).

Based on eqn. (71), the condition of increased focal prey density when all three species exist before and after building the MPA is:

$$F_P < \frac{c a_S^2 - c a_S a_N q}{e a_N} F_N \quad (73)$$

Because predator density increases and predation on alternative prey is stronger than on focal prey, alternative prey could go to extinction after building the MPA (eqn. (67) ≤ 0). Under this situation, the equilibrium densities of focal prey and predator after building the MPA are the same as eqns. (22)-(23) in Appendix S1 (focal prey density after building the MPA is: $N_M^* = \frac{\mu_P}{c a_N}$). Then, the condition of increased focal prey density in area B1 and B2 is:

$$N_M^* - N_0^* = \frac{\mu_P}{c a_N} - \frac{a_S^2(r_N - \mu_N - F_N) - a_S a_N(r_S - \mu_S - q F_N) + \frac{e}{c} a_N(\mu_P + F_P)}{e(a_S^2 + a_N^2)} \geq 0$$

That is:

$$F_P = \frac{c a_S^2 - c a_S a_N q}{e a_N} F_N + \frac{\mu_P(a_S^2 + a_N^2)}{a_N^2} - \frac{c a_S^2(r_N - \mu_N)}{e a_N} + \frac{c a_S(r_S - \mu_S)}{e} - \mu_P \quad (74)$$

Therefore, if predators don't drive alternative prey to extinction in the MPA (a_S is not large enough to make eqn. (67) ≤ 0), the condition of increased focal prey in area B1 and B2 (Fig. S1) after the creation of the MPA is eqn. (73). If predators strongly attack alternative prey to extinction in the MPA (a_S is large enough to make eqn. (67) ≤ 0), the condition of increased focal prey density in area B1 and B2 is eqn. (74). Under parameters in Table 1, alternative prey density after the creation of the MPA is always extinct when predator and focal prey exist in the MPA, so the increased focal prey condition in area B1 and B2 here is eqn. (74).

If fishing on prey is very large, all three components—predator, focal prey and alternative prey could go to extinction before building the MPA. Under this situation (by setting eqn. (62) ≤ 0), focal prey density always increases after building the MPA (area G in Fig. S1):

$$F_N > \frac{r_S - \mu_S}{q} \quad (75)$$

If fishing on prey is large to drive focal prey go to extinction but not too large to deplete alternative prey before the MPA, establishment of MPA will also increase focal prey density.

The conditions are gotten by setting eqn. (63) ≤ 0 but eqn. (62) > 0 (area F in Fig. S1):

$$r_N - \mu_N \leq F_N \leq \frac{r_S - \mu_S}{q} \quad (76)$$

If fishing on prey is not large enough to drive focal prey to extinction but only deplete predators before building the MPA ($F_N < r_N - \mu_N$; focal prey “before” density would be $N_0^* = \frac{r_N - \mu_N - F_N}{e}$ by solving eqn. (59) with $P = 0$), the condition of increased focal prey would be:

$$N_M^* - N_0^* = \frac{\mu_P}{ca_N} - \frac{r_N - \mu_N - F_N}{e} \geq 0, \text{ which indicates } r_N - \mu_N > F_N \geq r_N - \mu_N - \frac{\mu_P e}{ca_N} \text{ (gray dot-dash}$$

line, representing area E2 in Fig. S1).

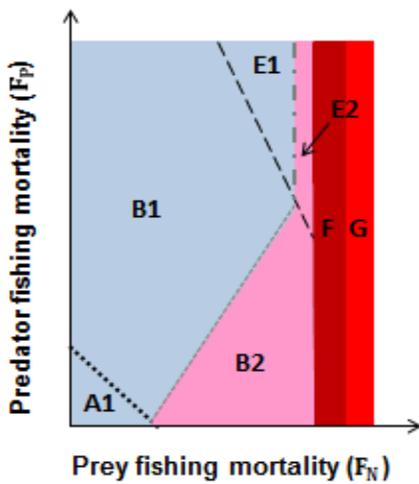


Fig. S1. Responses of focal prey density to MPAs’

establishment under different fishing rates

combinations in the absence of movement. There are

7 regions: A1: alternative prey goes to extinction

before and after the creation of the MPA (area below

the black dotted line –eqn. (66)); B1 and B2: all the

three species are extant before building the MPA but

only predator and focal prey are extant after building

the MPA; E1 and E2: focal and alternative prey are extant before building the MPA but only

predator and focal prey are extant after building the MPA (area above the black dashed line—

eqn. (65)); and F and G: focal prey is extinct before building the MPA but extant after building

the MPA (eqns. (75) and (76)). These regions differ in whether the focal prey decreases (blue

regions: A1, B1, E1) or increases (pink regions: B2, E2, F, G) in density after building the MPA.

The gray dotted line, separating B2 from B1, is $F_P = \frac{ca_S^2 - ca_S a_N q}{ea_N} F_N + \frac{\mu_P (a_S^2 + a_N^2)}{a_N^2} - \frac{ca_S^2 (r_N - \mu_N)}{ea_N} +$

$\frac{ca_S (r_S - \mu_S)}{e} - \mu_P$, and the gray dot-dash line, dividing E1 and E2, is $F_N = r_N - \mu_N - \frac{\mu_P e}{ca_N}$. Detailed

calculations are in Appendix S4.

**APPENDIX S5: ANALYSIS OF EFFECTS OF PREDATOR MOVEMENT IN GENERALIST PREDATOR (TWO-
PREY) MODEL**

If only predator post-settlement movement is considered, the equations (9)-(14) becomes

$$\dot{N}_M = r_N N_M - e N_M^2 - \mu_N N_M - a_N N_M P_M \quad (77)$$

$$\dot{S}_M = r_S S_M - e S_M^2 - \mu_S S_M - a_S S_M P_M \quad (78)$$

$$\dot{P}_M = c(a_N N_M P_M + a_S S_M P_M) - \mu_P P_M + m_P (P_F - P_M) \quad (79)$$

$$\dot{N}_F = r_N N_F - e N_F^2 - \mu_N N_F - a_N N_F P_F - F_N N_F \quad (80)$$

$$\dot{S}_F = r_S S_F - e S_F^2 - \mu_S S_F - a_S S_F P_F - F_S S_F \quad (81)$$

$$\dot{P}_F = c(a_N N_F P_F + a_S S_F P_F) - \mu_P P_F - F_P P_F + m_P (P_M - P_F) \quad (82)$$

where $F_S = qF_N$ (qF_N is used in the following).

At the equilibrium, the solutions are:

$$N_M^* = \frac{a_S^2(r_N - \mu_N) - a_N a_S(r_S - \mu_S) + \frac{e}{c} a_N \mu_P - \frac{e m_P}{c} a_N \left(\frac{1}{\rho} - 1\right)}{e(a_N^2 + a_S^2)} \quad (83)$$

$$N_F^* = \frac{a_S^2(r_N - \mu_N - F_N) - a_N a_S(r_S - \mu_S - qF_N) + \frac{e}{c} a_N (\mu_P + F_P) - \frac{e m_P}{c} a_N (\rho - 1)}{e(a_N^2 + a_S^2)} \quad (84)$$

$$S_M^* = \frac{a_N^2(r_S - \mu_S) - a_N a_S(r_N - \mu_N) + \frac{e}{c} a_S \mu_P - \frac{e m_P}{c} a_S \left(\frac{1}{\rho} - 1\right)}{e(a_N^2 + a_S^2)} \quad (85)$$

$$S_F^* = \frac{a_N^2(r_S - \mu_S - qF_N) - a_N a_S(r_N - \mu_N - F_N) + \frac{e}{c} a_S (\mu_P + F_P) - \frac{e m_P}{c} a_S (\rho - 1)}{e(a_N^2 + a_S^2)} \quad (86)$$

$$P_M^* = \frac{a_N(r_N - \mu_N) + a_S(r_S - \mu_S) - \frac{e}{c} \mu_P + \frac{e m_P}{c} \left(\frac{1}{\rho} - 1\right)}{a_N^2 + a_S^2} \quad (87)$$

$$P_F^* = \frac{a_N(r_N - \mu_N - F_N) + a_S(r_S - \mu_S - qF_N) - \frac{e}{c} (\mu_P + F_P) + \frac{e m_P}{c} (\rho - 1)}{a_N^2 + a_S^2} \quad (88)$$

where $\rho = \frac{P_M^*}{P_F^*}$ as before, by setting eqns. (87) over (88) = ρ , we can get a equation of ρ and m_P :

$$\rho = \frac{a_N(r_N - \mu_N) + a_S(r_S - \mu_S) - \frac{e}{c} \mu_P + \frac{e m_P}{c} \left(\frac{1}{\rho} - 1\right)}{a_N(r_N - \mu_N - F_N) + a_S(r_S - \mu_S - qF_N) - \frac{e}{c} (\mu_P + F_P) + \frac{e m_P}{c} (\rho - 1)} \quad (89)$$

which leads to $G(\rho, m_P)$ as:

$$(1 - \rho) \left[a_N(r_N - \mu_N) + a_S(r_S - \mu_S) - \frac{e}{c} \mu_P \right] + \rho \left(a_N F_N + a_S qF_N + \frac{e}{c} F_P \right) + \frac{e m_P}{c} \left(\frac{1}{\rho} - 1 \right) (1 + \rho^2) = 0 \quad (90)$$

To fit the above equation, we need $\rho > 1$.

From eqn. (90), we have:

$$\frac{\partial G}{\partial \rho} = - \left[a_N(r_N - \mu_N) + a_S(r_S - \mu_S) - \frac{e}{c} \mu_P - a_N F_N - a_S qF_N - \frac{e}{c} F_P \right] - \frac{e m_P}{c} \left(\frac{1}{\rho^2} + 2\rho - 1 \right) < 0$$

$$\frac{\partial G}{\partial m_P} = \frac{e(1-\rho)(1+\rho^2)}{c\rho} < 0 \quad (91)$$

From implicit differentiation, we have:

$$\frac{\partial \rho}{\partial m_P} = -\frac{\frac{\partial G}{\partial m_P}}{\frac{\partial G}{\partial \rho}} < 0 \quad (92)$$

From $G(\rho, m_P)$, we also get:

$$\begin{aligned} \frac{em_P}{c} \left(\frac{1}{\rho} - 1 \right) &= \frac{-[a_N(r_N - \mu_N) + a_S(r_S - \mu_S) - \frac{e}{c}\mu_P]}{1 + \rho^2} \\ &+ \frac{\rho[a_N(r_N - \mu_N) + a_S(r_S - \mu_S) - \frac{e}{c}\mu_P - a_N F_N - a_S q F_N - \frac{e}{c}F_P]}{1 + \rho^2} \\ \text{So } \frac{\partial P_M^*}{\partial \rho} &\propto \frac{\partial \left[\frac{em_P}{c} \left(\frac{1}{\rho} - 1 \right) \right]}{\partial \rho} = \frac{(2\rho + 1 - \rho^2)[a_N(r_N - \mu_N) + a_S(r_S - \mu_S) - \frac{e}{c}\mu_P] + (\rho^2 - 1)[a_N F_N + a_S q F_N + \frac{e}{c}F_P]}{(1 + \rho^2)^2} \\ &> \frac{(2\rho + 1 - \rho^2 + \rho^2 - 1)[a_N F_N + a_S q F_N + \frac{e}{c}F_P]}{(1 + \rho^2)^2} = \frac{2\rho[a_N F_N + a_S q F_N + \frac{e}{c}F_P]}{(1 + \rho^2)^2} > 0 \end{aligned}$$

$$\text{which leads to } \frac{\partial P_M^*}{\partial m_P} < 0 \quad (93)$$

$$\text{and } \frac{\partial N_M^*}{\partial m_P} \propto \frac{\partial \left[-\frac{em_P}{c} \left(\frac{1}{\rho} - 1 \right) \right]}{\partial \rho} > 0 \quad (94)$$

$$\text{when } m_P \rightarrow \infty, \lim_{m_P \rightarrow \infty} N_M^* = \frac{a_S^2(r_N - \mu_N) - a_N a_S(r_S - \mu_S) + \frac{1}{2}a_N a_S q F_N + \frac{e}{c}a_N \mu_P + \frac{1e}{2c}a_N F_P + \frac{1}{2}a_N^2 F_N}{e(a_N^2 + a_S^2)} \quad (95)$$

$$\lim_{m_P \rightarrow \infty} S_M^* = \frac{a_N^2(r_S - \mu_S) - a_N a_S(r_N - \mu_N) + \frac{1}{2}a_S a_N F_N + \frac{e}{c}a_S \mu_P + \frac{1e}{2c}a_S F_P + \frac{1}{2}a_S^2 q F_N}{e(a_N^2 + a_S^2)} \quad (96)$$

$$\lim_{m_P \rightarrow \infty} P_M^* = \frac{a_N(r_N - \mu_N) + a_S(r_S - \mu_S) - \frac{e}{c}\mu_P - \frac{1}{2}a_N F_N - \frac{1}{2}a_S q F_N - \frac{1e}{2c}F_P}{a_N^2 + a_S^2} = \lim_{m_P \rightarrow \infty} P_F^* > P_0^* \quad (97)$$

where P_0^* is the equilibrium predator density before the creation of the MPA (eqn. (64) in Appendix S4). This means that MPA establishment always increases predator density.

After building the MPA, without predator movement, predator density increases, which drives the alternative prey to extinction (eqn. (67) < 0 in Appendix S4 based on parameters in Table 1), but when predator movement increases, especially as $m_P \rightarrow \infty$, more and more alternative prey can be released, so there will be fishing rates where all three species exist after the creation of the MPA. By setting $\lim_{m_P \rightarrow \infty} S_M^* = 0$, we can find this threshold condition of F_N and F_P where alternative prey can rebound after the creation of the MPA when predator movement is infinite (blue line in Fig. S1):

$$F_P = -\frac{ca_N + ca_S q}{e} F_N + \frac{2ca_S a_N(r_N - \mu_N) - 2ca_N^2(r_S - \mu_S)}{ea_S} - 2\mu_P \quad (98)$$

Under this line (eqn. (98)), only predator and focal prey are extant after building the MPA when predator move infinitely, so the equilibrium density of focal prey after the creation of

the MPA becomes $\lim_{m_P \rightarrow \infty} N_M^* = \frac{1}{ca_N} \left[\mu_P + \frac{F_P}{2} + \frac{ca_N}{2e} F_N \right]$ (eqn. (52) in Appendix S3). There are two scenarios for the density of the focal prey before the creation of the MPA:

1. Predator and both prey are extant before building the MPA (area B1 and B2 in Fig. S1), so the focal prey density before building the MPA (N_0^*) is eqn. (63) in Appendix S4.

Thus, the condition of increased focal prey density after building the MPA is (area B2 in Fig. S1):

$$\lim_{m_P \rightarrow \infty} N_M^* - N_0^* = \frac{1}{ca_N} \left[\mu_P + \frac{F_P}{2} + \frac{ca_N}{2e} F_N \right] - \frac{a_S^2(r_N - \mu_N - F_N) - a_S a_N(r_S - \mu_S - qF_N) + \frac{e}{c} a_N(\mu_P + F_P)}{e(a_S^2 + a_N^2)} \geq 0$$

That is,

$$F_P \geq - \frac{ca_N a_S^2 + ca_N^3 + 2ca_N a_S^2 - 2ca_N^2 a_S q}{e(a_S^2 - a_N^2)} F_N - \frac{2ea_S^2 \mu_P - 2ca_N a_S^2 (r_N - \mu_N) + 2ca_N^2 a_S (r_S - \mu_S)}{e(a_S^2 - a_N^2)} \quad (99)$$

2. Only predator and focal prey are extant before the creation of the MPA (area A1 and A2 in Fig. S1), so the focal prey “before” density is eqn. (17) in Appendix S2, this scenario is the same as the specialist predator case where alternative prey goes to extinction before and after building the MPA, so the condition of increased focal prey density is eqn. (56) ($F_P < \frac{ca_N}{e} F_N$) in Appendix S3.

Above the blue line (eqn. (98)), predator and both prey species exist after the creation of the MPA, so the focal prey density after the creation of the MPA with infinite predator movement is eqn. (95). There are three scenarios of focal prey density before the creation of the MPA:

1. Predator and both prey species are extant before building the MPA (area C1 and C2 in Fig. S1), so the focal prey density before building the MPA (N_0^*) is eqn. (63) in Appendix S4. Thus, the condition of increased focal prey density after building the MPA is (area C2 in Fig. S1):

$$\lim_{m_P \rightarrow \infty} N_M^* - N_0^* = \frac{a_S^2(r_N - \mu_N) - a_N a_S(r_S - \mu_S) + \frac{1}{2} a_N a_S q F_N + \frac{e}{c} a_N \mu_P + \frac{1e}{2c} a_N F_P + \frac{1}{2} a_N^2 F_N}{e(a_N^2 + a_S^2)} - \frac{a_S^2(r_N - \mu_N - F_N) - a_N a_S(r_S - \mu_S - qF_N) + \frac{e}{c} a_N(\mu_P + F_P)}{e(a_N^2 + a_S^2)} = \frac{F_N \left(a_S^2 + \frac{1}{2} a_N^2 - \frac{1}{2} a_N a_S q \right) - \frac{1e}{2c} a_N F_P}{e(a_N^2 + a_S^2)} \geq 0$$

That is,

$$F_P \leq \frac{a_S^2 + \frac{1}{2} a_N^2 - \frac{1}{2} a_N a_S q}{\frac{1e}{2c} a_N} F_N \quad (100)$$

2. Only predator and focal prey are extant before building the MPA (area A3 in Fig. S3), so the focal prey density before building the MPA is given by eqn. (17) in Appendix S1; thus, focal prey density increases (under infinite predator movement) if:

$$\lim_{m_P \rightarrow \infty} N_M^* - N_0^* = \frac{a_S^2(r_N - \mu_N) - a_N a_S(r_S - \mu_S) + \frac{1}{2} a_N a_S q F_N + \frac{e}{c} a_N \mu_P + \frac{1}{2c} a_N F_P + \frac{1}{2} a_N^2 F_N}{e(a_N^2 + a_S^2)} - \frac{\mu_P + F_P}{c a_N} =$$

$$\frac{(\frac{1}{2} c a_N^2 a_S q + \frac{1}{2} c a_N^3) F_N - (\frac{1}{2} e a_N^2 + e a_S^2) F_P + c a_N a_S^2 (r_N - \mu_N) - c a_N^2 a_S (r_S - \mu_S) - e a_S^2 \mu_P}{c a_N (e(a_N^2 + a_S^2))} \geq 0$$

That is:

$$F_P \leq \frac{\frac{1}{2} c a_N^2 a_S q + \frac{1}{2} c a_N^3}{\frac{1}{2} e a_N^2 + e a_S^2} F_N + \frac{c a_N a_S^2 (r_N - \mu_N) - c a_N^2 a_S (r_S - \mu_S) - e a_S^2 \mu_P}{\frac{1}{2} e a_N^2 + e a_S^2} \quad (101)$$

Condition of eqn. (101) covers area A3 (in Fig. S3), and we conclude that focal prey density is always increases after building the MPA (i.e., the trophic cascade is reversed) throughout area A3 in Fig. S1.

3. Predator is extinct but the two prey species are extant before building the MPA (area E2 in Fig. S1), so the focal prey density will increase after building the MPA if:

$$\lim_{m_P \rightarrow \infty} N_M^* - N_0^* = \frac{(r_N - \mu_N) a_S^2 - a_N [a_S (r_S - \mu_S) - \frac{1}{2} a_S q F_N - \frac{e}{c} \mu_P - \frac{1}{2c} F_P - \frac{1}{2} a_N F_N]}{e(a_N^2 + a_S^2)} - \frac{r_N - \mu_N - F_N}{e} \geq 0$$

That is:

$$F_P \geq \frac{-c(a_S q + a_N + 2a_N + 2\frac{a_S^2}{a_N})}{e} F_N + \frac{2c a_N (r_N - \mu_N) + 2c a_S (r_S - \mu_S)}{e} - 2\mu_P \quad (102)$$

Thus, focal prey density always increases after building the MPA within the parameter space E2 in Fig. S3.

In Figs. S2 and S3, we give additional results of our simulations under different movement rates of predators, alternative prey, and larvae for intermediate fishing rates on the predator. In both figures, we selected parameter values that were strategically selected to represent areas that we knew from our other analyses to be sensitive to predator movement (i.e., parameters combinations that always resulted in trophic cascades (in the absence of movement of prey) vs. combinations that led to a transition from trophic cascades to increases in prey density as predator movement increased.

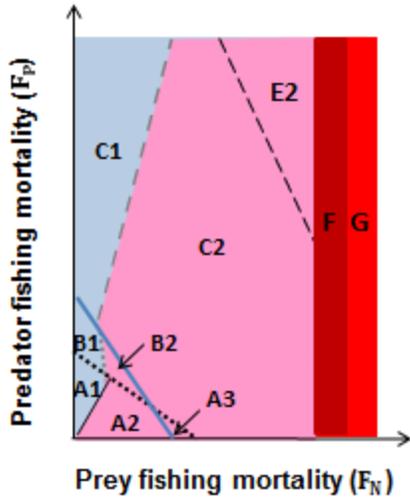


Fig. S1 Change in the density of focal prey after creation of the MPA in relation to fishing rates on the predator and prey when predators move infinitely ($m_p = \infty \text{ yr}^{-1}$). The parameter space can be divided into 10 regions: A1 and A2: alternative prey is always extinct before and after building the MPA, which is similar as specialist predator case; A3: alternative prey is extinct before building the MPA, but extant after building the MPA (if migration is allowed to facilitate

recolonization); B1 and B2: all three species are extant before building the MPA but only the predator and focal prey are extant after building the MPA; C1 and C2: all three species are extant before and after building the MPA; E2: two prey are extant before building the MPA and all three species are extant after building the MPA; and F and G: focal prey is extinct before building the MPA and extant after building the MPA (eqns. (75) and (76) in Appendix S4), where focal prey density always increase after the creation of the MPA, as the same in Appendix S4: Fig. S1. Beside of area F and G, other area is delineated by the blue line (eqn. (98)), black dotted line (eqn. (66) in Appendix S5) and black dashed line (eqn. 65 in Appendix S4).

Furthermore, these regions differ in whether the focal prey decreases (blue regions: A1, B1, C1) or increases (pink regions: A2, A3, B2, C2, E2) in density after building the MPA. As $m_p \rightarrow \infty$,

the solid black line, separating A1 from A2, is $F_p = \frac{ca_N}{e}$ (eqn. (56) in Appendix S3); the gray

dotted line that separates B1 from B2, converges to $F_p = -\frac{ca_N a_S^2 + ca_N^3 + 2ca_N a_S^2 - 2ca_N^2 a_S q}{e(a_S^2 - a_N^2)} F_N -$

$\frac{2ea_S^2 \mu_P - 2ca_N a_S^2 (r_N - \mu_N) + 2ca_N^2 a_S (r_S - \mu_S)}{e(a_S^2 - a_N^2)}$ (eqn. (99)); the gray dashed line, dividing C1 from C2,

converges to $F_p = F_N \frac{a_S^2 + \frac{1}{2}a_N^2 - \frac{1}{2}a_N a_S q}{\frac{1}{2c}a_N}$ (eqn. (100)). Note that trophic cascades are reversed in the

pink/red regions and this reversal is facilitated by infinite movement of the predator (by

comparing to Appendix S4: Fig. S1). The detailed calculations are in Appendices S4 and S5.

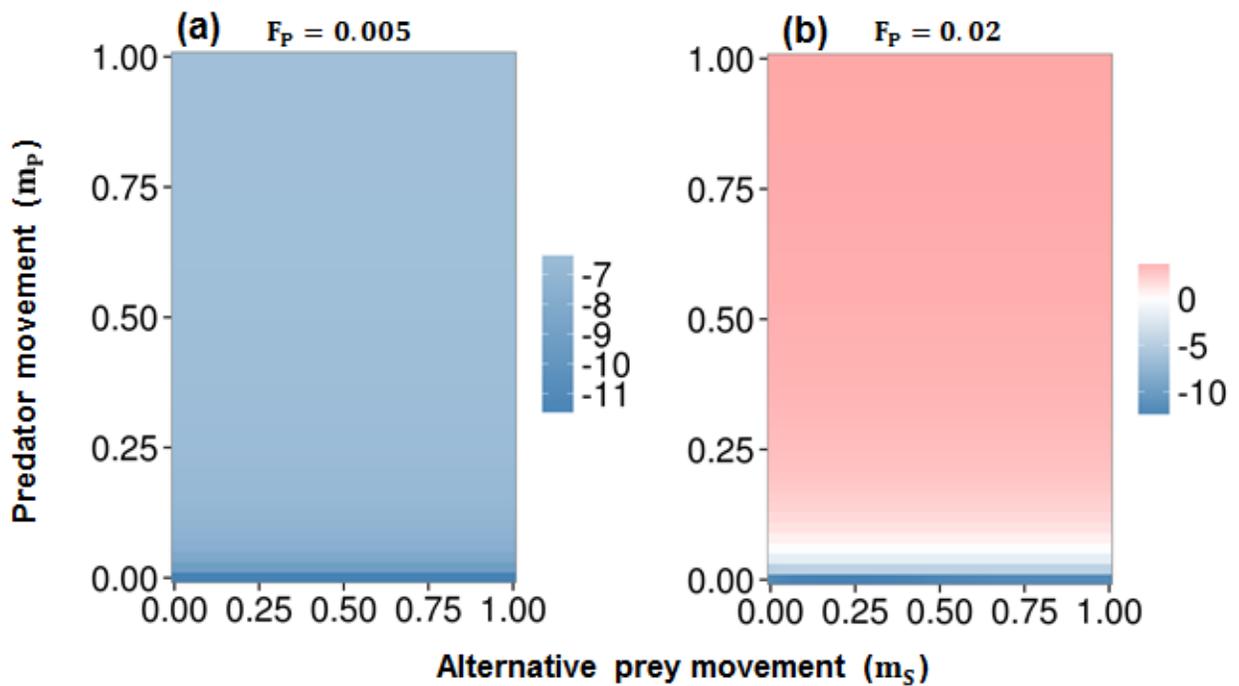


Fig. S2 Influence of alternative prey and predator movement rates (m_S and m_P) on the change of focal prey density before and after the creation of the MPA in the absence of larval connectivity ($p = 0$) under two different levels of fishing mortality on predator with constant fishing mortality on prey $F_N = 0.2$: a) $F_P = 0.005 \text{ yr}^{-1}$; b) $F_P = 0.02 \text{ yr}^{-1}$. Colors indicate the direction of change in focal prey density: increased focal prey density is indicated by red whereas decreased focal prey density is indicated by blue. Parameters were chosen to illustrate the effect of prey movement for different baseline situations in Fig. 6d (i.e., panel a used fishing rates that correspond to parameters in which the conditions always resulted in decreased focal prey density (blue region in Fig. 6d); whereas panel b used fishing rates where the focal prey response shifted from negative to positive as m_P increased (e.g., F_P and F_N fall into the red region of Fig. 6d). All the other parameter values are given in Table 1.

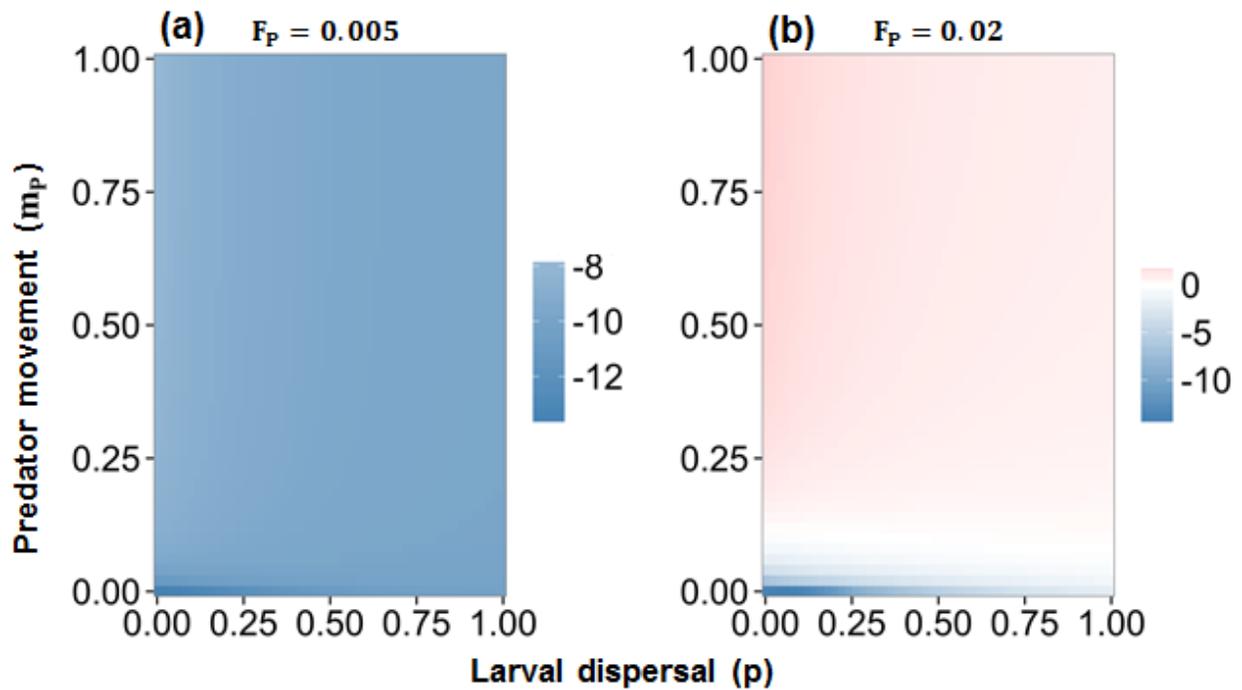


Fig. S3 Effects of larval dispersal (p) and predator movement rate (m_p) on the change in focal prey density after the creation of the MPA in the absence of prey movement (i.e., $m_N = 0$ and $m_S = 0$) and fishing mortality (i.e., $F_N = 0$) under two different levels of predator fishing mortality: a) $F_p = 0.005 \text{ yr}^{-1}$; b) $F_p = 0.02 \text{ yr}^{-1}$. Increased focal prey density is indicated by red whereas decreased focal prey density is indicated by blue. All the other parameter values are given in Table 1.

APPENDIX S6: SIMULATIONS OF EFFECT OF PREDATOR MOVEMENT ON PREY SIZE REFUGE AND

PREDATOR DENSITY-DEPENDENT MORTALITY WHEN $F_N=5F_P$ IN THE FINAL MODEL

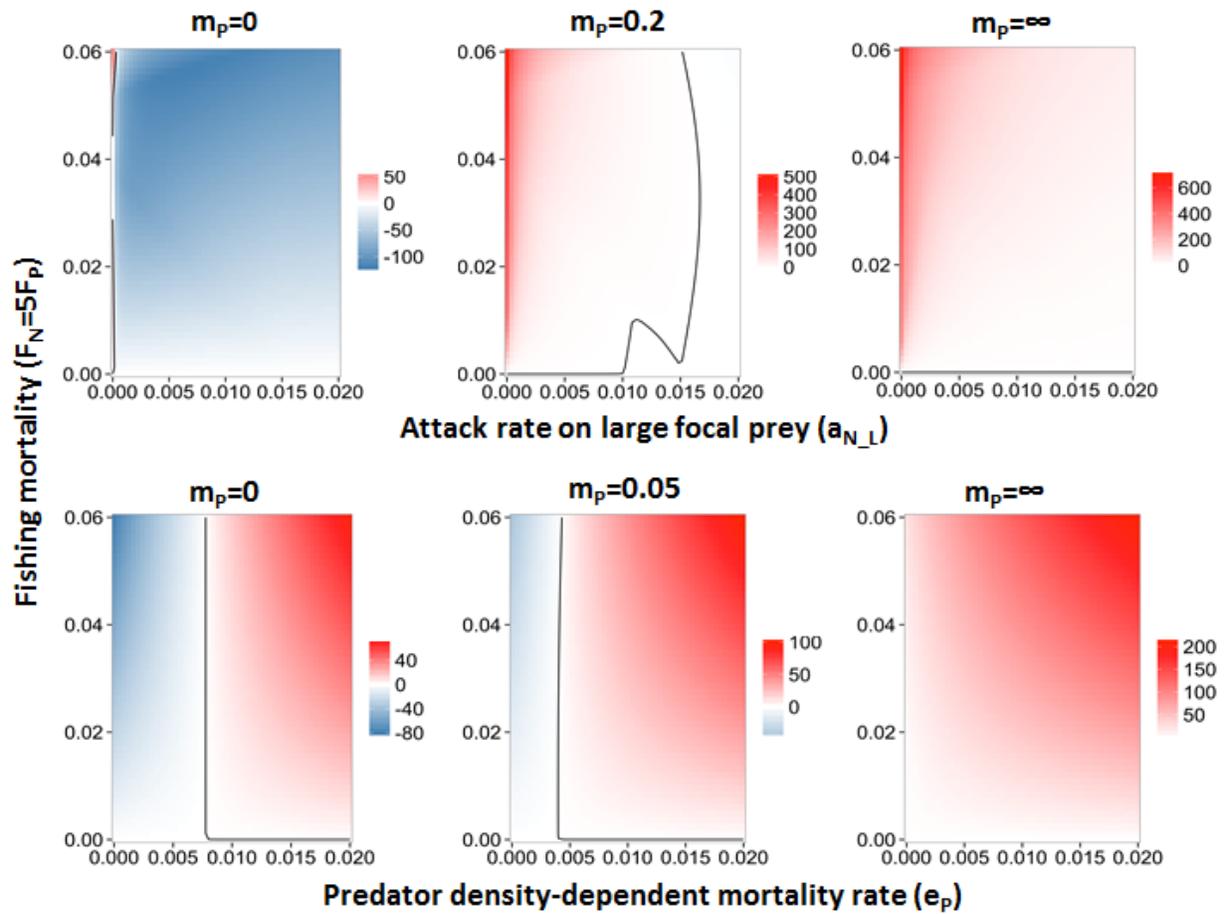


Fig. S1 Change in the density of focal prey (N_S+N_L) from before to after the creation of MPAs in relation to fishing mortality rate and either the magnitude of the prey size refuge for the large prey (panels a, b, c) or changes in the predator's density-dependent mortality (panels d, e, f) for three predator movement rates. In all cases, fishing rate on prey is five times that on predator ($F_N = 5F_P$). Colors indicate the direction of change in focal prey density after building the MPA: blue indicates decreased prey density, whereas red indicates increased prey density. Black lines, which separate the above two, show parameter combinations that yield no change in focal prey density from before to after building the MPA. Other parameter values are given in Table 1.