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ORIGINAL ARTICLE

Paradox of marine protected areas: suppression of fishing may cause species loss

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Abstract A number of fish and invertebrate stocks have been depleted by overexploitation in recent years. To address this, marine protected areas (MPAs) are often established to protect biodiversity and recover stocks. We analyzed the potential impact of establishing MPAs on marine ecosystems using mathematical models. We demonstrate that establishment of an MPA can sometimes result in a considerable decline, or even extinction, of a species. We focus on a prey–predator system in two patches, one exposed to fishing activity and the other protected (MPA). Our analyses reveal that the establishment of the MPA can cause a reduction in prey abundance, and even extinction of the prey. Such unintended consequences are more likely to occur if the predator species is a generalist and if the MPA is intended to protect only the predatory species. Further, a mobile predator that migrates adaptively rather than randomly is associated with a greater reduction in prey abundance.

Keywords Adaptive migration · Fisheries · Fishing scheme · Marine reserve · Trophic cascade

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Introduction

In recent years, a number of fish and invertebrate stocks have been depleted by overexploitation, and many are in danger of extinction (Botsford et al. 1997). To protect biodiversity and recover stocks, researchers or managers often recommend the establishment of marine reserves or marine protected areas (MPAs) (Palumbi 2001; Botsford et al. 2003). However, scientific evidence of the effects of marine reserves is still not sufficient (Roberts et al. 2005). Traditionally, fishery management and marine conservation have been based on models that have a single-species perspective (Gerber et al. 2003; Matsuda and Abrams 2006). Although these models are useful in revealing the key elements of complex ecosystems, they are sometimes ineffective because they ignore other factors, such as spatial structure or species interactions (Pikitch et al. 2004).

Harvest can significantly alter the trophic structure in marine systems by direct removal of biomass and introduction of a strong bias in the species impacted (Pauly et al. 1998; Baskett et al. 2007). That is, fisheries generally have a greater effect on larger, slower-growing, and longer-lived species (Jennings et al. 1998; Heino and Godo 2002). Similarly, MPAs can influence the population size of multiple species and modify the structure of whole communities through a suite of direct and indirect effects (Salomon et al. 2002; Micheli et al. 2004; Baskett et al. 2006). The effects of fishing are also partly dependent on the migratory capacity of the species (Botsford et al. 2003). Therefore, an understanding of the effects of MPAs on target species requires models that include multiple species and spatial structures.

The effect of MPAs has been evaluated using models that differ in the modes of competition, age structure, and larval dispersal. Most of these studies have concluded that the establishment of MPAs eventually increased fishing yields or net social benefits (e.g., Quinn et al. 1993; Guenette and Pitcher 1999; Hastings and Botsford 1999; Mangel 2000; Halpern 2003; Steele and Beet 2003; Ami et al. 2005; Baskett 2006; White et al. 2008; Merino et al. 2009; but see e.g., Walters 2000; Salomon et al. 2002; Micheli et al. 2004; Walters et al. 2007; Kellner and Hastings 2009). Conversely, some researchers have reported declines in prey population size within existing MPAs (e.g., Sala and Zabala 1996; Shears and Babcock 2002; Langlois and Ballantine 2005). For example, Shears and Babcock (2002) estimated that the likelihood of predation by a predatory species, which is protected within MPAs in northeastern New Zealand, was approximately seven times higher than outside the reserve. As a result, the abundance of their prey (sea urchins) was significantly lower at reserve sites.

Pinnegar et al. (2000) reviewed the likelihood of trophic cascade effects in benthic marine ecosystems following the establishment of MPAs. The authors suggested that species composition may change over time and that some species may be extirpated as the abundance of predator species increased (Tilman 1982; Hixon 1991; Graham et al. 2003, 2007; McClanahan et al. 2007).

A similar phenomenon has been widely reported in terrestrial ecosystems where a reduction in human activity is associated with a loss of species. For instance, where the landscape has been modified by human activity for hundreds of years, a recent decrease in anthropogenic land-use often results in species loss. This is regarded as one of the most important causes of a loss of biodiversity (e.g., Kobori and Primack 2003; Katoh et al. 2009; Yamaura et al. 2009). We suspect that a similar process may occur in marine ecosystems that have been subject to intensive human exploitation (e.g., fishing) for hundreds of years. Indeed, we hypothesize that there may be a decline in species abundance or diversity following the introduction of MPAs that suppress fishing activities.

In this paper we explore the potentially negative effects of introducing an MPA. We analyze a prey–predator system in two patches, one exposed to fishing activity (fishing ground) and the other protected (MPA). In this model, the abundance of the prey may decline and the prey may become extinct after the MPA is established. We show that only a generalist predator can cause extinction of the prey. We also examine the case in which different species are targeted for fishing and protection. The possibility of extinction of the prey species in response to the MPA depends on the choice of species exposed to fishing pressure and the migration rates of the species. Last, we examine the situation in which the species tend to concentrate in an area that confers higher fitness (adaptive migration).

Model

We consider a simple prey–predator system. Because the majority of marine consumers are generalists (Micheli et al. 2004), we consider the case in which the predator is a generalist that has an alternative food source other than the prey species in the model. Before the MPA is established, the population dynamics of the two species are expressed by the following differential equations:

$$\dot{x} = r_x x\left(1 - \frac{x}{K_x}\right) - axy - c_x x - q_x E_x x, \tag{1a}$$

$$\dot{y} = r_y y\left(1 - \frac{y}{K_y}\right) + \theta axy - c_y y - q_y E_y y, \tag{1b}$$

where x and y are the population sizes of the prey and predator, respectively, on the fishing ground. r_i is the per capita reproductive rate, and K_i is the carrying capacity of species i ($i = x, y$). For simplicity, we consider the type I functional response: the predator captures the prey at a rate proportional to prey abundance with rate coefficient a, and this contributes to an increase in the predator population with a conversion rate of θ. c_i represents the density-independent natural death rate of species i.

The first and the second terms on the right-hand side of Eq. 1b correspond to the population growth of the generalist predator. The first term comes from the alternative food resource and the second term comes from the prey. These two growth terms are separated in our model, which indicates that population growth caused by feeding on the prey does not immediately affect their carrying capacity (K_y). In S1 of the Electronic Supplementary Material (ESM), we explain the derivation of this functional form of the population growth rate of the generalist predator. Some theoretical studies of generalist predators have adopted an alternative model for a generalist predator in which the second growth factor is immediately dependent on the carrying capacity (K_y) (e.g., Holt 1977; Kellner et al. 2010). We have conducted all the analyses with this alternative functional form and confirmed that the conclusions are qualitatively the same as when using a model with Eqs. 1a, b, as discussed in S1 of the ESM.

The last terms on the right–hand side of Eqs. 1a, b represent the loss due to fishing. Here, the harvest is assumed to be proportional to the abundance of the targeted stocks (x or y), as is commonly assumed in fishery resource management models. q_i and E_i represent the catchability coefficient and harvest effort, respectively, for species i (Clark 1990).

If the predator is a specialist, there is no contribution by the alternative prey, and hence the first term on the right-hand side of Eq. 1b is zero.

To model the effect of establishing an MPA, we consider a system composed of two areas: the fishing ground and the no-take zone (i.e., the MPA). These two areas are connected by the migration of the two species (Fig. 1). We represent the fractions of these areas as $1-R$ and R, respectively, where $0 \le R \le 1$. If $R = 0$, there is no MPA, which corresponds to Eqs. 1a, b. If $R = 1$, all species are protected in the area of concern, and the model becomes Eqs. 1a, b with no fishing mortality ($E_x = E_y = 0$). For an intermediate value of R, the carrying capacities of these two areas are proportional to their sizes. We first consider the case in which the prey and the predator migrate between the two areas randomly at migration rate m_i $(i = x, y)$, which may differ between species. The rates of emigration and immigration also depend on the size of the areas.

The population dynamics of the two species in the presence of an MPA are:

$$\dot{x}_1 = r_x x_1\left(1 - \frac{x_1}{(1-R)K_x}\right) - \frac{a x_1 y_1}{1-R} - c_x x_1 - q_x E_x x_1 + m_x[(1-R)x_2 - Rx_1], \tag{2a}$$

$$\dot{x}_2 = r_x x_2\left(1 - \frac{x_2}{RK_x}\right) - \frac{a x_2 y_2}{R} - c_x x_2 + m_x[Rx_1 - (1-R)x_2], \tag{2b}$$

$$\dot{y}_1 = r_y y_1\left(1 - \frac{y_1}{(1-R)K_y}\right) + \frac{\theta a x_1 y_1}{1-R} - c_y y_1 - q_y E_y y_1 + m_y[(1-R)y_2 - Ry_1], \tag{2c}$$

$$\dot{y}_2 = r_y y_2\left(1 - \frac{y_2}{RK_y}\right) + \frac{\theta a x_2 y_2}{R} - c_y y_2 + m_y[Ry_1 - (1-R)y_2], \tag{2d}$$

where x_n and y_n represent the population sizes of the prey and predator, respectively, in area n $(n = 1, 2)$. Areas 1 and 2 represent the fishing ground and MPA, respectively. The last terms in Eqs. 2a–d express the exchanges among populations of the prey or predator between two patches. m_x and m_y represent the migration rates of the prey and predator. Here, we assume random migration, in which fish are more likely to migrate to the larger patch in proportion to the relative size of the patch. Explanations of the migration terms are given in S2 of the ESM. Note that the first, third, and last terms in Eqs. 2a–d have R or $1-R$ in the denominator. This dependence on R is most easily understood by transforming the dynamics of population size to the dynamics of density (see S1 in ESM). We can also explain this formulation in a more intuitive way. For example, the dependence on R of the second term on the right-hand side of Eq. 2a is a function of the rate of predation per individual predator being equal to a[prey density]. This should be converted to the form $ax_1/(1-R)$, where x_1 is the number of prey individuals in the focal area (fishing ground). The reader might suspect that it may increase as R becomes closer to 1, though this is not the case. When the fraction of the area open to fishing becomes smaller, $1-R$ becomes smaller, but the number of individuals on the fishing ground also decreases if the density remains the same. Taking this result, the rate of predation loss of prey individuals per unit time is $ax_1y_1/(1-R)$, which corresponds to the second term in Eq. 2a.

In the following, we examine how introduction of an MPA affects the population size of two species.

Equilibrium and prey extinction

Here, we consider a situation in which both species are the targets of harvest on the fishing ground, and both are

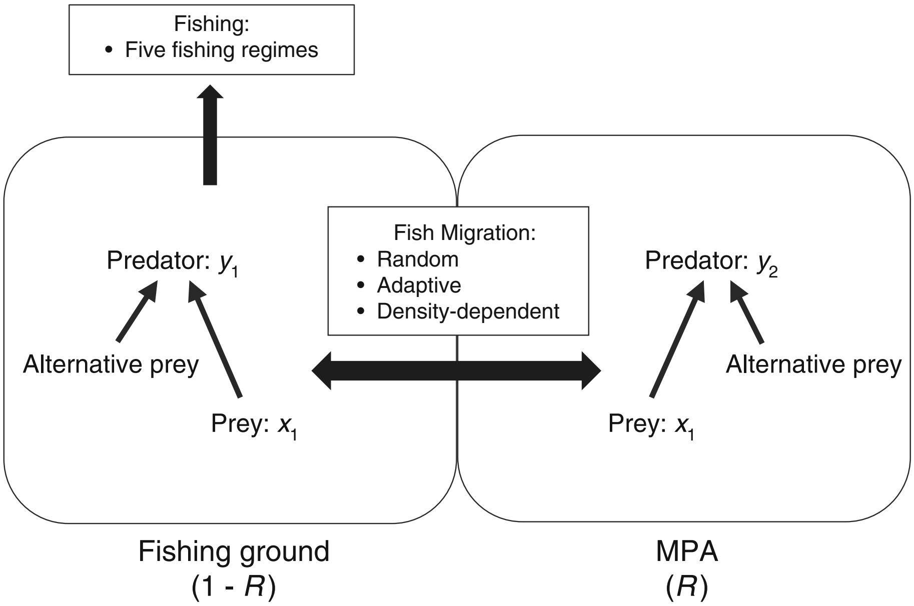

Fig. 1 Schematic description of the model

protected in the MPA. Hereafter, we call this case I; other cases will be discussed later (see Table 1). We find that the introduction of the MPA either increases the abundance of both species or increases the predator's abundance, but can also decrease the prey's abundance. The latter is known as a trophic cascade effect (Pinnegar et al. 2000; Kellner et al. 2010).

According to the mathematical analyses in S3 of the ESM, the trophic cascade occurs when inequality $aK_y/r_y > q_xE_x/q_yE_y$, $(r_y \neq 0)$ is satisfied. Note that this inequality is independent of migration rates.

When the trophic cascade effect is very strong, the establishment of an MPA can even cause extinction of the prey as R, the fraction of the MPA, increases (see Fig. 2). When the prey is sedentary or slowly migrating ($m_x = 0.1$ and 1, respectively), the prey is less likely to go extinct when the ratio of the predator's migration rate to the prey's migration rate m_y/m_x is very small (Fig. 2a, b). As the ratio m_y/m_x increases, extinction of the prey becomes more likely to occur. The peak of the extinction curve occurs at a point when the predator's migration rate, m_y, is approximately 10 times greater than that of the prey in Fig. 2a, and when it is approximately equal to the prey's migration rate, m_x in Fig. 2b. However, the extinction curves exhibit very little variation in m_y/m_x in a scenario where the prey migrates rapidly ($m_x = 10$ and 100) (Fig. 2c, d, respectively).

The conditions for the prey's extinction can be derived mathematically from the local stability analysis (see S4 in ESM) and also graphically by comparing the locations of the prey and predator isoclines on the prey–predator phase plane at $R = 0$ and $R = 1$ (see S3 in the ESM).

We also examined the case in which the migratory pattern is controlled by density dependence (see Conrad 1999; Greenville and MacAulay 2007), as explained in S2 of the ESM. However, the qualitative conclusion remains the same as for the example of density-independent migration (see Fig. S2 in the ESM).

Specialist versus generalist predators

As stated above, most marine consumers are generalists (Micheli et al. 2004). However, a number of specialist predators also exist. In this section, we examine the case in which the predator is a specialist, and compare the results with those for a generalist predator (see prior section).

If the predator is a specialist, the prey population always declines and the predator always increases as the fraction of the total area protected increases. Namely, a trophic cascade effect always occurs (see also S3 in the ESM). Figure 3 illustrates a scenario in which the equilibrium population abundance of the prey declines after the introduction of the MPA. The prey's migration rate (m_x) is the same as in Fig. 2. We can see that the prey is sedentary and slowly migrating for $m_x = 0.1$ and 1, respectively (Fig. 3a, b). The prey is moderately fast migrating and fast migrating for $m_x = 10$ and 100, respectively (Fig. 3c, d). Although the equilibrium population abundance of the total prey changed with the ratio m_y/m_x, the specialist predator never caused extinction of the prey, irrespective of the migration rates of the two species (Fig. 3). The reason is intuitively clear—when the prey is rapidly consumed, and its abundance becomes very low, the abundance of its specialist predator decreases owing to prey shortages, which prevents the extinction of the prey.

The term r_y provides an index for the degree to which a species is a generalist, which indicates the intrinsic population growth rate conferred by the alternative resources only. $r_y = 0$ implies that the predator is a specialist. Figure 4 illustrates that, as r_y decreases, a larger MPA is needed to cause extinction of the prey, and that with $r_y = 0$, the prey's extinction never occurs. Therefore, only a generalist predator can cause extinction of the prey, and the probability of extinction increases as the predator depends more strongly on alternative resources. Note that these results are derived from a deterministic model. However in real ecosystems, even a specialist predator can

Table 1 Summary of probable changes in five cases

Case	Fishing target in the open area	Fishing target in the MPA	Expected changes
I	Prey and predator	None	Predator increases, and prey either declines or increases
II	Prey and predator	Predator	Both prey and predator increase
III	Prey and predator	Prey	Prey declines and predator increases
IV	Prey	None	Both prey and predator increase
V	Predator	None	Prey declines and predator increases

Case I Both species are harvested before the MPA is established, and are protected by the MPA. *Case II* Both species are originally harvested, and only the prey is protected by the MPA. *Case III* Both species are originally harvested, and only the predator is protected by the MPA. *Case IV* Only the prey is originally harvested. *Case V* Only the predator is originally harvested

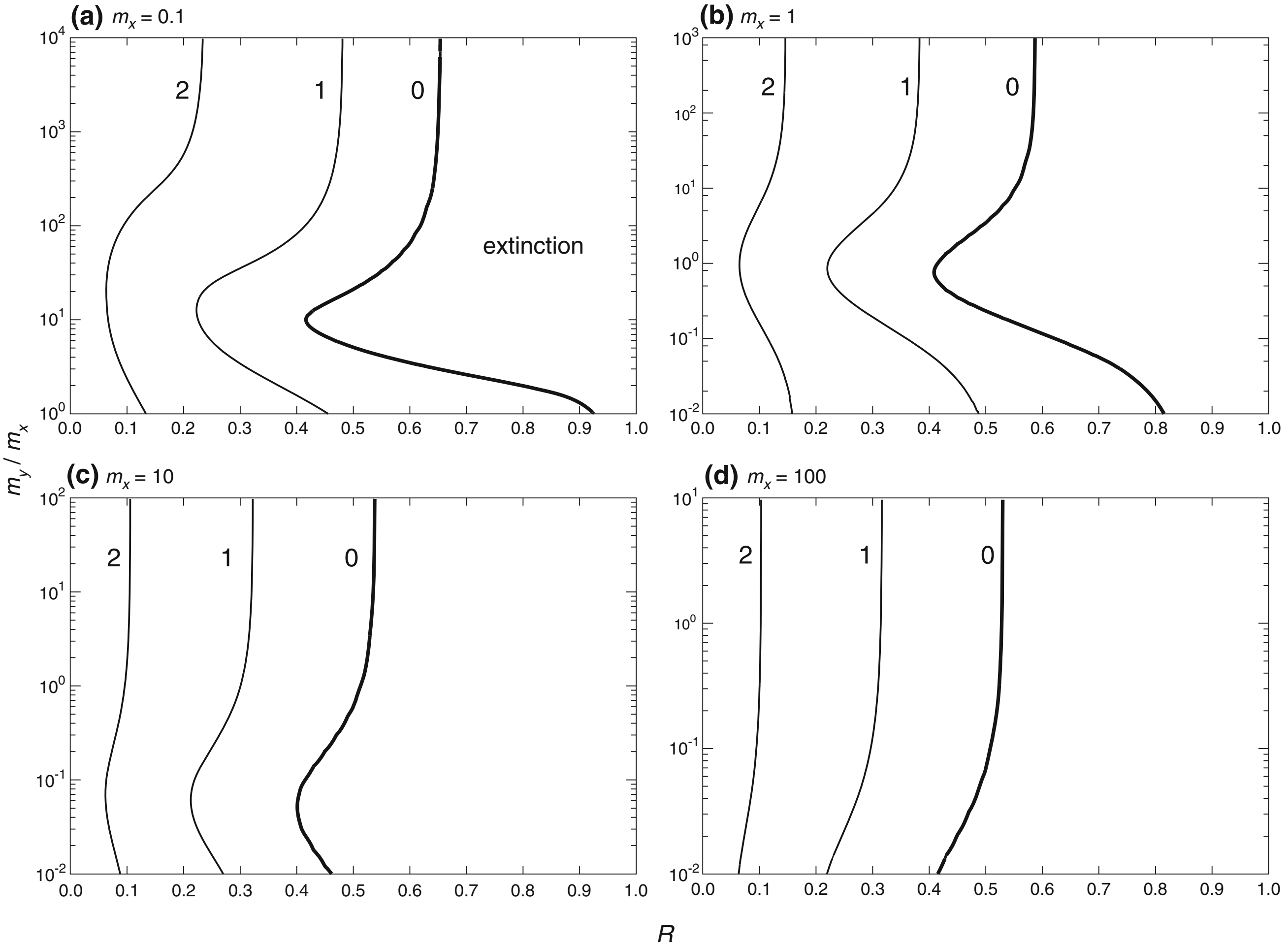

Fig. 2 Contour plots for the total prey population at equilibrium ($x_1^* + x_2^*$). The *horizontal axis* is R, the fraction of total area protected within an MPA. The *vertical axis* is the ratio of the predator's migration rate (m_y) to the prey's migration rate (m_x) in a logarithmic scale. The prey's migration rate differs among panels. Note that the range of predator's migration rate differs among panels. The areas to the *right of the bold lines* correspond to the parameter range for the prey's extinction. The total abundance of the prey decreases with the fraction of the area under protection (R). Other parameters are: $r_x = 2$, $r_y = 0.9$, $K_x = 40$, $K_y = 10$, $q_x = 1$, $q_y = 1$, $E_x = 0.7$, $E_y = 0.7$, $a = 0.3$, $\theta = 0.3$, $c_x = 0.1$, and $c_y = 0.1$

cause the extinction of a prey during times when prey abundance is very low owing to stochastic phenomena.

Alternative case scenarios

In the last section, we considered case I, in which both species are harvested and both are protected in the MPA. However, the results are likely to differ under different fishing regimes in the prey–predator model. Here, we consider the following four additional cases with different combinations of targeted and/or protected species (see also Table 1). We illustrate the results of these four cases by graphical analysis (see S3 in the ESM).

(II) Both species are originally harvested, and only the prey is protected in the MPA.

In this case, introducing the MPA always increases the abundance of both the prey and predator (Fig. 5a).

(III) Both species are originally harvested, and only the predator is protected in the MPA.

In this case, introducing the MPA causes the predator population to increase but the prey population to decrease (Fig. 5b).

(IV) Only the prey is originally harvested and it is protected in the MPA.

In this case, introducing the MPA always increases the abundances of both the prey and the predator. As a result, the total abundance always increases with R (Fig. 5c).

(V) Only the predator is originally harvested and it is protected in the MPA.

In this case, introducing the MPA causes the predator to increase but the prey to decrease (Fig. 5d).

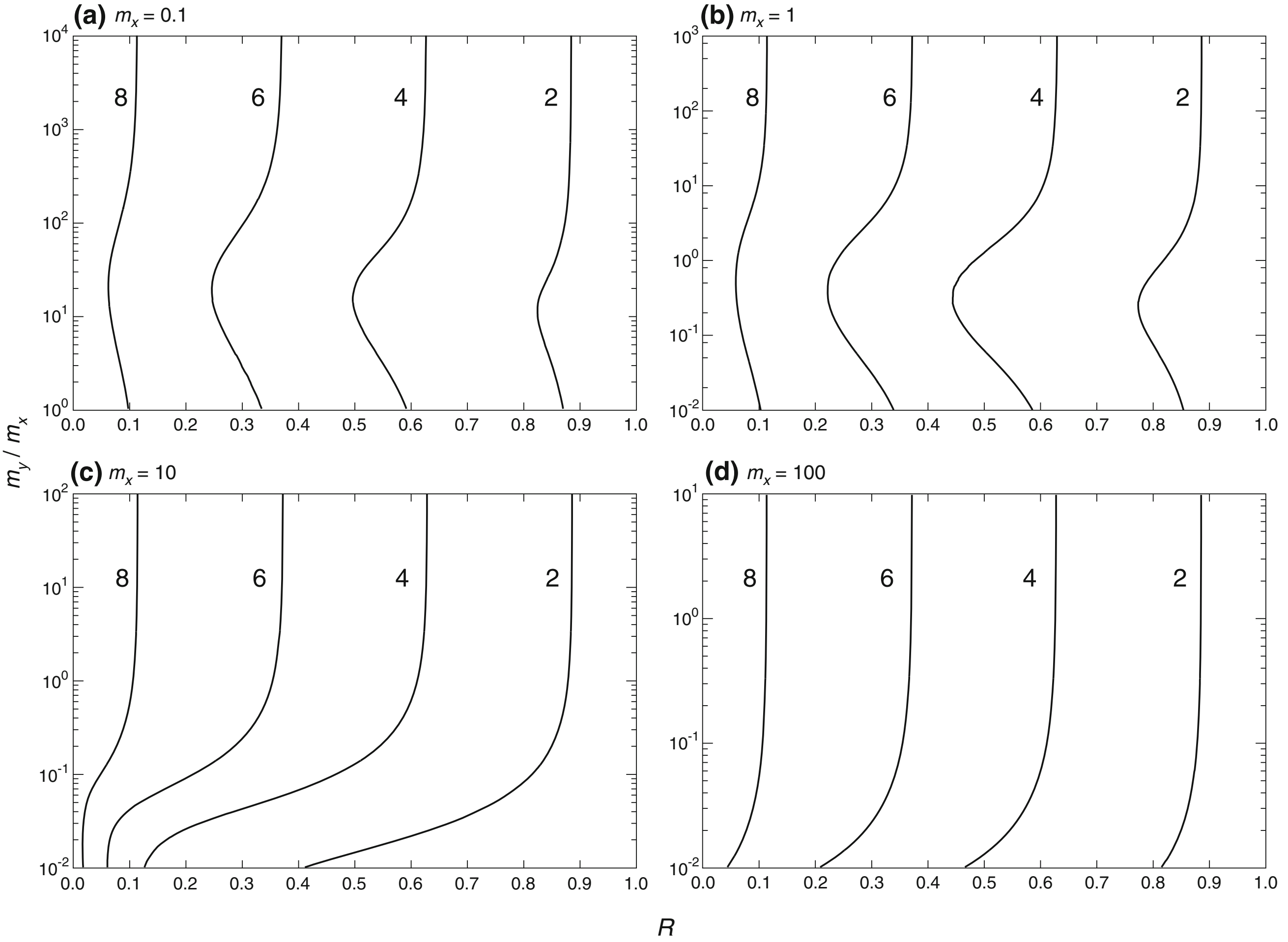

Fig. 3 Contour plots for the total prey population at equilibrium ($x_1^* + x_2^*$). The *horizontal axis* is R, the fraction of total area protected within an MPA. The *vertical axis* is the ratio of the predator's migration rate (m_y) to the prey's migration rate (m_x) in a logarithmic scale. m_x and m_y are the same as in Fig. 2. The total abundance of the prey decreases with R but it never reaches zero. Other parameters are: $r_x = 2$, $r_y = 0.9$, $K_x = 40$, $K_y = 10$, $q_x = 1$, $q_y = 1$, $E_x = 0.7$, $E_y = 0.7$, $a = 0.3$, $\theta = 0.3$, $c_x = 0.1$, and $c_y = 0.1$

In all cases, the predator abundance (y) increases as the fraction of area covered by the MPA (R) increases. While the change in the equilibrium abundance of the prey differs among the cases described above: (1) the prey abundance increases only if the prey is protected, as in cases II and IV; (2) the prey abundance decreases only if the predator is protected, as in cases III and V; and in case I, (3) the prey abundance may either increase or decrease concomitantly with the size of the MPA, depending on the choice of parameters (see S3 in the ESM). These predictions are summarized in Table 1.

Adaptive migration in fish

Thus far, we have assumed that both species migrate randomly between the two areas. However, many animals are capable of some degree of habitat choice (e.g., Abrams 2000, 2007; Doligez and Pärt 2008; Wang and Takeuchi 2009). In this section, we consider a situation in which the species migrate in an adaptive manner. Individuals tend to migrate to more suitable habitat based on differences in the fitness conferred by the two habitats.

Here, to illustrate the effect of adaptive migration, we focus on case I, in which both species are harvested before the introduction of the MPA, and both are protected in the MPA (Table 1). We consider the conditions under which the prey becomes extinct, and compare the results for adaptive migration with those for random migration.

Effect of adaptive migration on the likelihood of the prey's extinction

As an index to show the likelihood of the prey's extinction, we use the size of the parameter region in Fig. 2 that

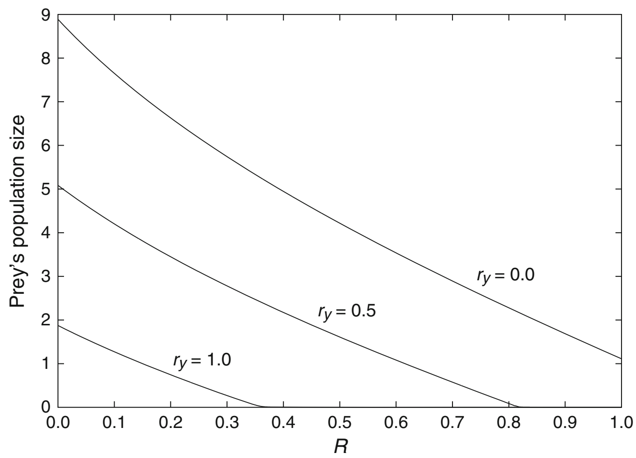

Fig. 4 Prey population size at equilibrium. The *horizontal axis* is *R*. *Different curves* correspond to different r_y, which indicates the availability of an alternative food source. A large r_y indicates that the predator is a generalist. The population size of the prey becomes smaller as r_y increases. The generalist predator can cause the extinction of the prey, and the possibility of its extinction increases as r_y increases. Parameters are: $r_x = 2$, $K_x = 40$, $K_y = 10$, $q_x = 1$, $q_y = 1$, $E_x = 0.7$, $E_y = 0.7$, $m_x = 1$, $m_y = 2$, $a = 0.1$, $\theta = 0.3, c_x = 0.1$, and $c_y = 0.1$

caused the prey's extinction. Using this extinction likelihood index we discuss the effect of adaptive migration.

Figure 6 illustrates the relative size of the area of the parameter region in which the prey's extinction occurs on an $R - m_y/m_x$ plane. The size of the prey's extinction area in Fig. 2 is normalized to 1, which corresponds to the value at $\beta_x = \beta_y = 0$ in Fig. 6. Here, β_i $(i = x, y)$ is a measure of sensitivity to the fitness difference between the two patches (see S2 in the ESM).

Figure 6a illustrates the effects of adaptive migration by the prey (i.e., $\beta_x \geq 0$, $\beta_y = 0$). If only the prey migrates adaptively, the size of the prey's extinction region is smaller than if both species migrate randomly ($\beta_x = \beta_y = 0$). In addition, the size of the parameter region corresponding to extinction becomes smaller as the adaptiveness of the prey (β_x) increases (Fig. 6a).

In general, adaptive migration by the prey ($\beta_x \geq 0$) decreases the likelihood of extinction because they choose to stay in a patch that has reduced risk of both fishing and predation. Prey that have high levels of adaptiveness (β_x) have reduced likelihood of extinction.

Figure 6b illustrates the case in which only the predator migrates adaptively ($\beta_x = 0$, $\beta_y \geq 0$). If the prey is sedentary or slow migrating ($m_x = 0.1$, 1, respectively), the size of the parameter region for the prey's extinction increases when the adaptiveness of the predator (β_y) is small. However, β_y increases, the size of the parameter region for extinction decreases, and the prey become less likely to suffer extinction than in the case where both species migrate randomly ($\beta_x = \beta_y = 0$). If the prey is moderately fast migrating or fast migrating ($m_x = 10$, 100, respectively), the size of the parameter region for the prey's extinction is greater when the predator migrates adaptively than when it migrates randomly ($\beta_x = \beta_y = 0$; Fig. 6b).

We further examined the effect of the adaptiveness of the predator's migration by testing the effect of different migratory rates. We performed the analysis described above using three migratory rate ranges for the predator: (1) a sedentary predator, which has a migration rate of $0.1 \leq m_y \leq 1$; (2) a moderately fast migrating predator, which has a migration rate of $1 < m_y < 10$; and (3) a fast migrating predator, which has a migration rate of $10 \leq m_y \leq 100$. Our results suggest that a sedentary predator with an adaptive migration is always associated with a decreased likelihood of extinction of the predator. Conversely, the moderately fast migrating/fast migrating predators are associated with outcomes similar to those in Fig. 6b.

Discussion

We analyzed a simple mathematical model of a prey–predator system in two areas, one of which receives fishing activity (fishing ground) and another that does not (MPA). We evaluated the effects of introducing the MPA upon the ecosystem. When the MPA was established, the abundance of the predator species always increased. In contrast, depending on the fishing schemes and/or parameter set, the abundance of prey may increase or decrease in abundance (Table 1, S3 in the ESM). Interestingly, protection of the predator in the MPA can lead to extinction of the prey. We derived the mathematical conditions for this to occur. If the predator is a specialist rather than a generalist, the prey never becomes extinct. The extinction of the prey is more likely to occur as the availability of an alternative food source for the predator increases (Fig. 4).

We also examined situations in which alternative species were targeted by the fishery and were protected in the MPA. Our results fall into three types: (1) prey abundance increases when only the prey is protected (case II and case IV); (2) prey abundance declines when only the predator is protected (case III and case V); and (3) prey abundance can either increase or decrease as the area covered by the MPA is increased or decreased, depending on the choice of parameters (case I, see also S3 in the ESM). Predator abundance always increases, irrespective of these differences (Table 1). Our results suggest that there are situations where the establishment of an MPA may cause an undesirable outcome, such as a reduction in the prey species (cases III and V). In these instances, the effort made to protect biodiversity may result in a decline, or even loss, of a prey species.

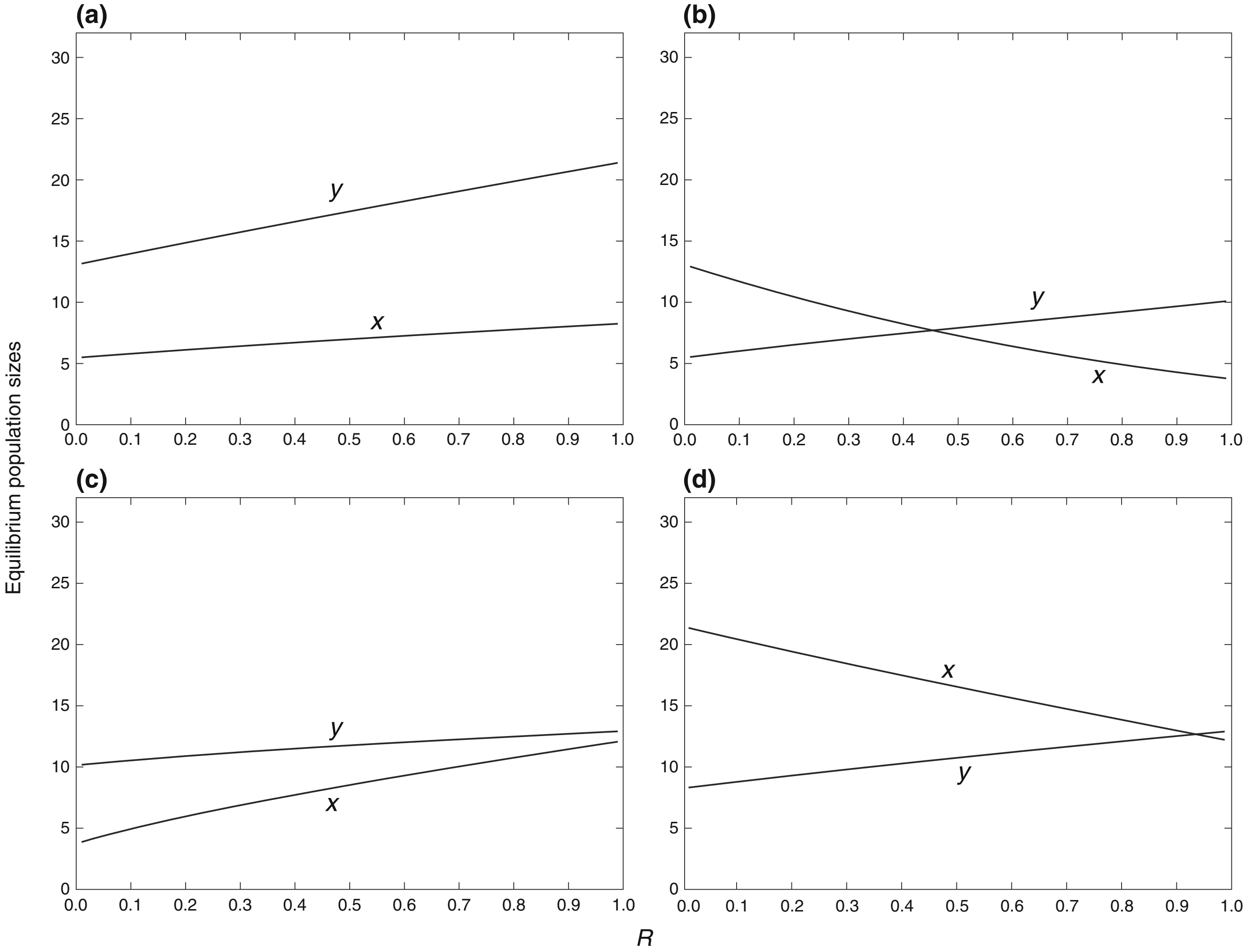

Fig. 5 Population sizes of the prey and predator at equilibrium. The different panels correspond to different cases of the target species under fishing and protection (see Table 1). (**a**) Case II, both species increase after only the prey is protected. (**b**) Case III, the predator increases, whereas the prey declines, after only the predator is protected. (**c**) Case IV, both species increase after fishing stops. (**d**) Case V, the predator increases, whereas the prey declines, after fishing stops. Parameters are: $r_x = 2$, $r_y = 0.9$, $K_x = 40$, $K_y = 10$, $q_x = 1$, $q_y = 1$, $E_x = 0.7$ for (**a**), (**b**), (**c**), $E_y = 0.7$ for (**a**), (**b**), (**d**), $m_x = 0.5$, $m_y = 0.5$, $a = 0.1$, $\theta = 0.3$, $c_x = 0.1$, and $c_y = 0.1$

We also considered situations in which the species migrate between patches in an adaptive manner. When only the prey migrates adaptively, the likelihood of the prey's extinction always decreases as the adaptive sensitivity of the prey increases (Fig. 6a). When only the predator migrates adaptively, the likelihood of the prey's extinction is either increased or decreased depending on the adaptiveness of the predator's migration (β_y) (Fig. 6b).

Our results can be understood intuitively in the context of trophic cascades during the implementation of MPAs (reviewed by Pinnegar et al. 2000). In food web theory (Paine 1966, 1971, 1974; Hughes 1994; Estes et al. 1998; Duffy and Hay 2001), the removal of a higher-order predator may allow other intermediate predators to increase in number, which in turn may have a negative impact on the prey species at a lower trophic level (Holt and Lawton 1994). In our model, the predator is always positively affected by the suppression of a fishery, even if the fishing intensity upon the predator is not changed. This is because suppression of the fishery on the prey tends to increase prey abundance. This effect becomes larger as the area protected by the MPA increases. However, the effect of fishery suppression on prey abundance varies with the type of fishery: either the fishery exploits only one species ("top predator" is a specialist) or exploits both species ("top predator" is a generalist). The suppression of the former type of fishery increases prey abundance. However, suppression of the latter type of fishery increases or decreases prey abundance depending on the relative strength of the positive and negative effect on the prey.

Our analysis demonstrates that introducing an MPA can lead to a reduction in biodiversity. This is consistent with

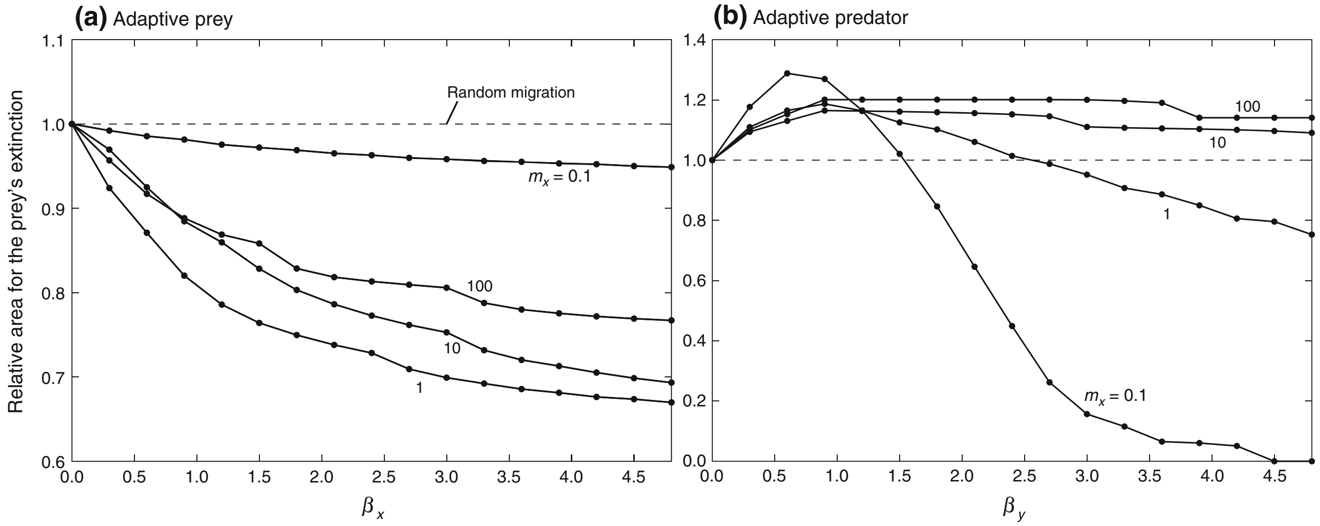

Fig. 6 Relative size of the area in the parameter space in which the prey becomes extinct (see Fig. 2). Note that the scales of the *vertical axes* are different between the panels. The size of the parameter region for the prey's extinction in Fig. 2 is divided by the value for $\beta_x = \beta_y = 0$. The *horizontal axis* is the degree of adaptiveness of migration (β_x or β_y). The *broken line* indicates 1 for random migration ($\beta_x = \beta_y = 0$). The values of migration rate of the prey differ between *four lines*, and are indicated by numbers: (**a**) The adaptive migration of the prey reduces the likelihood of the prey's extinction. (**b**) The likelihood of the prey's extinction is either increase or decrease, depending on the prey's migration rate, m_x, and the adaptiveness of the predator, β_y (see *text*). Other parameters are: $r_x = 2$, $r_y = 0.9$, $K_x = 40$, $K_y = 10$, $q_x = 1$, $q_y = 1$, $E_x = 0.7$, $E_y = 0.7$, $m_x = 1$, $m_y = 2$, $a = 0.3$, $\theta = 0.3$, $c_x = 0.1$, and $c_y = 0.1$

other theoretical studies that also suggest MPAs may have a negative impact (e.g., Walters 2000; Micheli et al. 2004; Kellner and Hastings 2009). For example, Micheli et al. (2004) examined a discrete time model in two patches of sedentary adults (only one of which was open to fishing), when the predator's larvae were mixed in the pelagic pool. Their prey stayed in each local patch. Based on computer simulations, the authors reported an unexpected decline in the predator population when a small fraction of the patch was protected (in a reserve). Kellner and Hastings (2009) further discussed the "reserve paradox", that introducing MPAs facilitates bioinvasion and invasive coexistence by increased spatial heterogeneities in the context of persistence of indigenous species.

Most previous theoretical studies into the effects of MPAs emphasize the single-species perspective (Gerber et al. 2003), and have generally illustrated the benefits of introducing MPAs. Based on our multi-species model, we observed an increase in predator abundance but a counterintuitive decline, and even extinction, of the prey in response to the MPA. The impacts of a fishery vary among species (Jennings et al. 1998; Heino and Godo 2002). Therefore, it is reasonable to expect that the benefits of MPAs would also vary among species. As a consequence, a decline in prey abundance is likely to be observed in a multispecies model.

Natural marine ecosystems are characterized by a given age and size structure of their constituent species, novel distribution patterns, unique water currents, and temporally fluctuating environments, among other aspects. We deliberately adopted a very simple model to demonstrate the potential for unexpected outcomes following establishment of an MPA. However such simple models can be misleading. Thus, there is a need to model the potential effects of MPAs using more realistic models that incorporate a variety of structures. We adopted the simplest functional response in which the prey feeding rate is proportional to the abundance of the prey. However, if the predator is a switching predator (Murdoch and Oaten 1975; Matsuda et al. 1986), the feeding rate will tend to decrease when the prey's abundance becomes low, resulting in a lower probability of extinction. Baskett (2006) noted that integrating prey size refugia lowers the likelihood of a trophic cascade following establishment of an MPA in a simple model with a specialist predator. More biologically realistic models that capture prey–predator dynamics are needed in future studies. For example, a number of fish species have a larval stage that recruits to stocks in very distant habitats (James et al. 2002; Leis et al. 2011), a phenomenon that is not considered in this paper. Such spatial structures should be taken into account when determining the potential effects of an MPA.

The major lessons we can learn from analysis of the simple model presented in this paper are as follows. First, introducing an MPA may cause loss of fish diversity, despite the intention that it is established to protect biodiversity. Therefore, we must be very cautious about potential outcomes of introducing an MPA in a community of interacting species, even though most existing theoretical studies of MPAs emphasize their positive effects. Second, the risk of the prey's extinction is greater if the target of the fishery is a predator species, and if the predator is a generalist. Last, the mode of migration (random, adaptive, or density-dependent migration) can significantly affect the likelihood of the prey's extinction. This alerts us to the need to understand the mode of migration of the species and their migratory capacity.

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