On the spillover effect and optimal size of marine reserves for fishing yields

Nao Takashina[1*]

[1] *Biodiversity and Biocomplexity Unit, Okinawa Institute of Science and Technology Graduate University, Onna-son, Okinawa 904-0495, Japan*

Abstract

Marine reserves are an essential component of model fisheries management. As implementing marine reserves induces an inherent tradeoff between the harvesting and conservation, to solidify the insight into fisheries management with marine reserves is fundamental for management success. Finding an optimal reserve size that improves the fishing yield is not only theoretical interest but also practically important to assess the underlying tradeoffs and to facilitate decision making. Also, since the species migration determines the degree of the spillover effect from a marine reserve, it is a key consideration to explore the performance of marine reserve. Here, we investigate an optimal reserve fraction and its management outcome under different levels of spillover via a simple two-patch mathematical model, in which one patch is open to fishing, and the other is protected from fishing activities. The two-patch model is approximated by a single population dynamics when the migration rate is sufficiently larger than the growth rate of a target species. In this limit, we show that an optimal reserve size exists when the pre-reserve fishing is operated at the fishing mortality larger than the f_{MSY}, the fishing mortality at the maximum sustainable yield (MSY). Also, the fishing yield with the optimal reserve size becomes as large as MSY in the limit. Numerical simulations across various migration rates between two patches suggest that the maximum harvest under the management with a marine reserve is achieved in this limit, and this contrasts with the conservation benefit in which is maximized at the intermediate migration rate.

1 Introduction

Marine reserves or no-take marine protected areas (MPAs) are a central tool in modern fisheries management to reduce fishing pressure and to preserve biodiversity [23, 35, 44]. As often an implementation of a marine reserve leads to a fishing closure, there is an inherent tradeoff between harvest and conservation [9, 27]. In addition, while one may postulate the

*Electronic address: nao.takashina@gmail.com

positive influence of marine reserve introductions, previous studies have revealed unintended outcomes, including species loss due to an altered species interaction strength [43], intensified fishing activity close to the reserve boundary [15, 26], and escalating the competitions among fishermen that suppresses the reserve benefit [40]. Hence, to solidify our insight into the effect of the marine reserve is fundamental for the robust design of a marine reserve establishment. Well-designed marine reserve networks can mitigate or even eliminate the tradeoff of marine reserve [12, 46] and having well-established guidelines for marine reserve design largely facilitates the management decision making.

Optimizing fishing yields is often one of the central concerns of marine reserve implementations (e.g., [21, 29]), and we refer to the *optimal size of marine reserves* in this sense throughout the paper. Of course, there exist various objects of marine reserves (e.g., biodiversity conservation [2] or improving ecological resilience [5, 41]) and, hence, the optimal size of marine reserves is context-dependent. One key consideration for its optimal implementation is the condition for the marine reserve to improve the fishing yield [7, 21, 38, 45]. In fact, marine reserves can merely reduce fishing yield when a fishery sustainably manages a stock [21, 24, 31, 47] or a target species has a high fecundity ability [38]. Previous studies suggested that the threshold for a marine reserve to increase the fishing yield is f_{MSY}, the fishing mortality at the maximum sustainable yield (MSY), including the model of population dynamics described by the stock-recruit relationship [21], bioeconomic model [30], and stage-structured model [31]. One key aspect complementing to the previous findings, in regarding the optimal reserve size, is the effect of the species migration between a marine reserve and fishing ground because previous studies focused on no adult movement [21, 38, 47] and well-mixed population [7, 45]. However, marine organisms show highly diverse mobility and dispersal behaviors, including density-dependent and independent (diffusion) migrations [18]. For instance, fish and echinoderms species often exhibit the density-dependent movement [1, 33] and these have considerable effects on the performance of marine reserves [18, 19, 28, 41]. Hence, investigating these effects on the optimal reserve size for the fishing yield and its relationship to the conservation benefit, such as population size, will further strengthen current insight.

Here, we investigate the optimal reserve size, which improves the fishing yield, with the effect of the spillover due to the species migration, and the realized conservation benefit measured by the total population size. The model is a simple two patch model where one patch represents the fishing ground and the marine reserve for the other. The species migration connects the two patches at a species-specific rate, and it affects the degree of the spillover from the marine reserve. This creates a source-sink dynamics between the fishing ground and marine reserve, and this is a common structure of existing spatially-explicit models (e.g., [10, 14, 29, 41]). The two patch model also allows us to examine different migration modes [3], such as the positive/negative density-dependent as well as density-independent migrations. This simple approach yields analytical results by introducing an aggregated model when the migration rate is sufficiently larger than the growth rate of a target species [4, 7, 25, 40, 42]. The aggregated model allows us to derive the condition for an optimal reserve size to exist and the fishing yield and total population size under the

management with the optimal reserve fraction. These suggest that an optimal reserve size exists when the fishing mortality is larger than the f_{MSY}, and the fishing yield and the total population size under the management correspond to MSY and X_{MSY}, the population size at MSY.

Numerical calculations across various migration rates suggest that the aggregated model gives the highest fishing yields among various species migration rates. That is, the well-mixed population with a large migration rate maximizes the fishing yield. On the other hand, our model shows that a marine reserve provides a larger total population, a measure of conservation benefit when the migration ability of a target species is low or moderate. These contrasting results emphasize the importance of the spillover effects in consideration of the tradeoffs under the management with marine reserves.

2 Model

2.1 Basic model

Our starting point is the commonly used Schaefer model [16, 37] where the population dynamics of the target species x is described with the growth rate r, carrying capacity K, and fishing mortality rate f as follows:

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - fx. \tag{1}$$

In this model, MSY, the fishing mortality rate at MSY, f_{MSY}, and the population size at MSY, X_{MSY}, are described as

$$\text{MSY} = \frac{rK}{4},\ f_{MSY} = \frac{r}{2},\ \text{and } X_{MSY} = \frac{K}{2}. \tag{2}$$

To investigate the effect of marine reserve, we employ a common two-patch model (e.g., [14, 41, 43]) where one patch is open to fishing ($i = 1$; with fraction $1 - \alpha$) and another patch ($i = 2$; with fraction α) is protected from fishing activity (i.e., $f = 0$), and the species migration connects the two patches (Fig. 1). With the migration function $M(x_1, x_2)$ where x_1 and x_2 are the population of fishing ground and marine reserve, respectively, Eq. (1) becomes

$$\frac{dx_1}{dt} = rx_1\left(1 - \frac{x_1}{(1-\alpha)K}\right) - fx_1 + M(x_1, x_2), \tag{3a}$$

$$\frac{dx_2}{dt} = rx_2\left(1 - \frac{x_2}{\alpha K}\right) - M(x_1, x_2), \tag{3b}$$

We consider the situation where migrations between the patches are either the random fashion or positive/negative density dependent. With the parameter controlling the migration model, s, we describe the migration function $M(x_1, x_2)$ as

$$M(x_1, x_2) = m\left\{\left(\frac{x_2}{\alpha K}\right)^s (1-\alpha)x_2 - \left(\frac{x_1}{(1-\alpha)K}\right)^s \alpha x_1\right\}, \tag{4}$$

where, the function represents the negative density-dependent migration when $-1 < s < 0$, random migration when $s = 0$, and density-dependent migration when $s > 0$ [3].

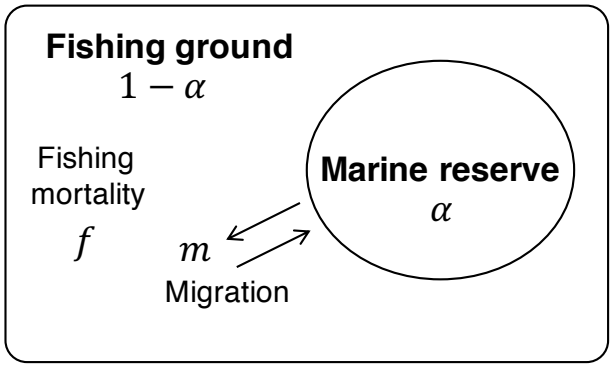

Figure 1: Schematic description of the model. The space is divided into the fishing ground (fraction $1-\alpha$) with fishing mortality, f, and the marine reserve (fraction α) without fishing activity. The species migration at a rate m connects the dynamics of two patches. Species migration is either positively/negatively density-dependent or density-independent.

We use the notations to describe the fishing yield and the total population size under the management with a marine reserve as

$$Y_{res} = fx_1, \text{ and } X_{res} = x_1 + x_2. \tag{5}$$

where, these quantities are used in the following to compare the management without marine reserve.

2.2 Model aggregation

When the migration rate is sufficiently larger than the growth rate ($m \gg r$), there are fast and slow dynamics operating at different time scales [4, 25]. Then, the migration term has a negligible effect on the total population $X = x_1 + x_2$ operated at the time scale of fast parameter $\tau = mt$. Thus, Eq. (3) can be approximated by a single aggregated model [42]

$$\frac{dX}{d\tau} = rX\left(1 - \frac{X}{K}\right) - f(1-\alpha)X. \tag{6}$$

In the following, we discuss the analytical aspect of the aggregated model (6), and perform numerical calculations across the species migration rate m including the situation where the model aggregation is not valid.

3 Results

3.1 Analysis of the aggregated model Eq. (6)

The aggregated model allows us to obtain explicit form of the equilibrium as follows:

$$\bar{X}^{AG} = K\left(1 - \frac{f(1-\alpha)}{r}\right), \tag{7}$$

and fishing yield is

$$\bar{Y}^{AG} = f(1-\alpha)K\left(1 - \frac{f(1-\alpha)}{r}\right), \tag{8}$$

where, the superscript AG indicates the equilibrium of the aggregated model. By solving $d\bar{Y}^{AG}/df = 0$ about f and α, respectively, we obtain the optimal fishing mortality and reserve size:

$$f^{AG*} = \frac{r}{2(1-\alpha)}, \tag{9}$$

$$\alpha^{AG*} = 1 - \frac{r}{2f}. \tag{10}$$

Eq. (9) suggests that one needs to increase the fishing mortality with a rate inversely proportional to the fraction of fishing ground $1-\alpha$ after an establishment of a marine reserve, and it becomes infinitely large when the fraction of the marine reserve approaches to unity (Fig. 2). On the other hand, Eq. (10) represents that for an (positive) optimal reserve size to exist the fishing yield should be larger than MSY level:

$$f > \frac{r}{2} = f_{MSY}. \tag{11}$$

In other words, if the fishing mortality is smaller than the MSY level, there is no optimal MPA size to improve fishing yield. Also, the optimal size approaches 1 (i.e., complete fishing ban) as the fishing mortality becomes large (Fig. 2).

From Eq. (6), we see the maximum fishing yields coincides to MSY of Eq. (1). In fact, substituting either Eq. (9) or (10) into Eq. (8) recovers Eq. (2). We denote this by

$$\bar{Y}^{AG*}|_{f^*} = \bar{Y}^{AG*}|_{\alpha^*} = \text{MSY}. \tag{12}$$

We often use notation $\bar{Y}^{AG*}$ when the substitution is obvious. Similarly, we regard $\bar{X}^{AG*}$ as the population size when fishing yield is given by Eq. (12).

3.2 Numerical investigation for general situation

When the migration rate is not large enough, then the aggregated model is not valid. Yet, we will show that the the analytical results above provides a maximum value of fishing yield, and it becomes a benchmark to discuss the performance of an introduced marine reserve.

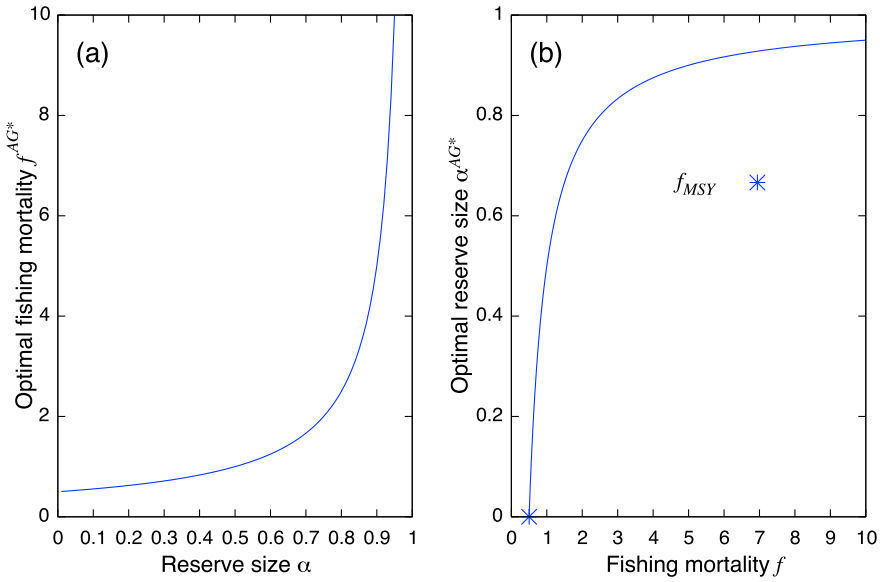

Figure 2: (a) Optimal fishing mortality of the aggregated model f^{AG*} (Eq. (9)) and (b) optimal reserve size α^{AG*} (Eq. (10)). Positive reserve size exists only when fishing mortality is larger than f_{MSY}.

Here, we numerically solve Eq. (3) to find the fishing yield and the optimal reserve size α^*, as well as total population size under various reserve sizes and migration rates. To compare these quantities with those of the management without marine reserve, we introduce the following two normalized quantities: the fishing yield normalized by the MSY, Y_{res}/MSY, and the total population size normalized by X_{MSY}, X_{res}/X_{MSY}. Note from the analysis above, the aggregated model under the optimal reserve size, α^{AG*}, gives the values of normalized fishing yield and population size $\bar{Y}^{AG*}/\text{MSY} = \bar{X}^{AG*}/X_{MSY} = 1$.

The top three panels in Figure 3 show the normalize fishing yield under the density-independent migration ($s = 0$). As expected, the optimal reserve size α^*, if any, approaches that of the aggregated model α^{AG*} as the migration rate m becomes large. Also, the normalized fishing yield of the aggregated model gives the upper bound: ($Y_{res}/\text{MSY} \leq \bar{Y}^{AG*}/\text{MSY}$). The numerical calculations also suggest that the condition for the positive optimal reserve size exists (Eq. 11) still holds for the various migration rate. Therefore, the improvement of fishing yield by introducing marine reserve occurs only when the initial fishing mortality exceeds the MSY level. Although this condition may be necessary for a marine reserve to increase the harvesting when the migration rate is not high enough, it does not guarantee the existence of an optimal reserve size. For example, when the fishing mortality rate is moderately high ($f = 0.75$; Figure 3b), the spillover effect from the marine reserve is necessary for an optimal reserve size to exist. The bottom three panels in Fig. 3 show the slice of the heat map shown in the top panels at $m = 0.1$, 1, or 10. The fishing mortality rate f

corresponds to the top panel. These represent that the fishing yield tends to be higher when the migration rate m is high. Also, there are peaks when the fishing mortality is larger than $f_{MSY} = 0.5$, and these correspond to the optimal reserve size α^*.

On the other hand, the bottom three panels of Figure 4 shows the normalized total population size. This value represents the conservation benefit of the marine reserve. The management with an optimal size of the marine reserve tends to give a smaller population size than X_{MSY} (i.e., $X_{res}/X_{MSY} < 1$). However, given the fishing mortality is larger than f_{MSY}, this value approaches 1, the prediction of the aggregation model, as the migration rate m becomes sufficiently large (Fig. 4b, c). Also, these show that an increasing the reserve size provides a higher normalized population size, and the population size becomes larger at low to moderate migration rates (m is about 1 in Figure 4) at a given reserve size. The bottom three panels in Fig. 4 show more explicitly this relationship when the migration rate is $m = 0.1$, 1, or 10. Unlike the fishing yields, the population size, a measure of conservation benefit, is larger when the migration rate is moderate ($m = 1$) than a high rate ($m = 10$). These suggest a mismatch between an optimal harvesting and conservation benefit.

We found the qualitatively similar trends in two alternative migration modes: density-dependent ($s = 1$; Fig. 5) and negatively density-dependent ($s = -0.5$; Fig. 6) migrations between patches where we show only the heat maps. Some quantitative difference appears around intermediate migration rates m is around 1, but these approach to the prediction of the aggregated model as the migration rate becomes sufficiently large, and optimal reserve size appear when the fishing mortality rate is larger than f_{MSY}.

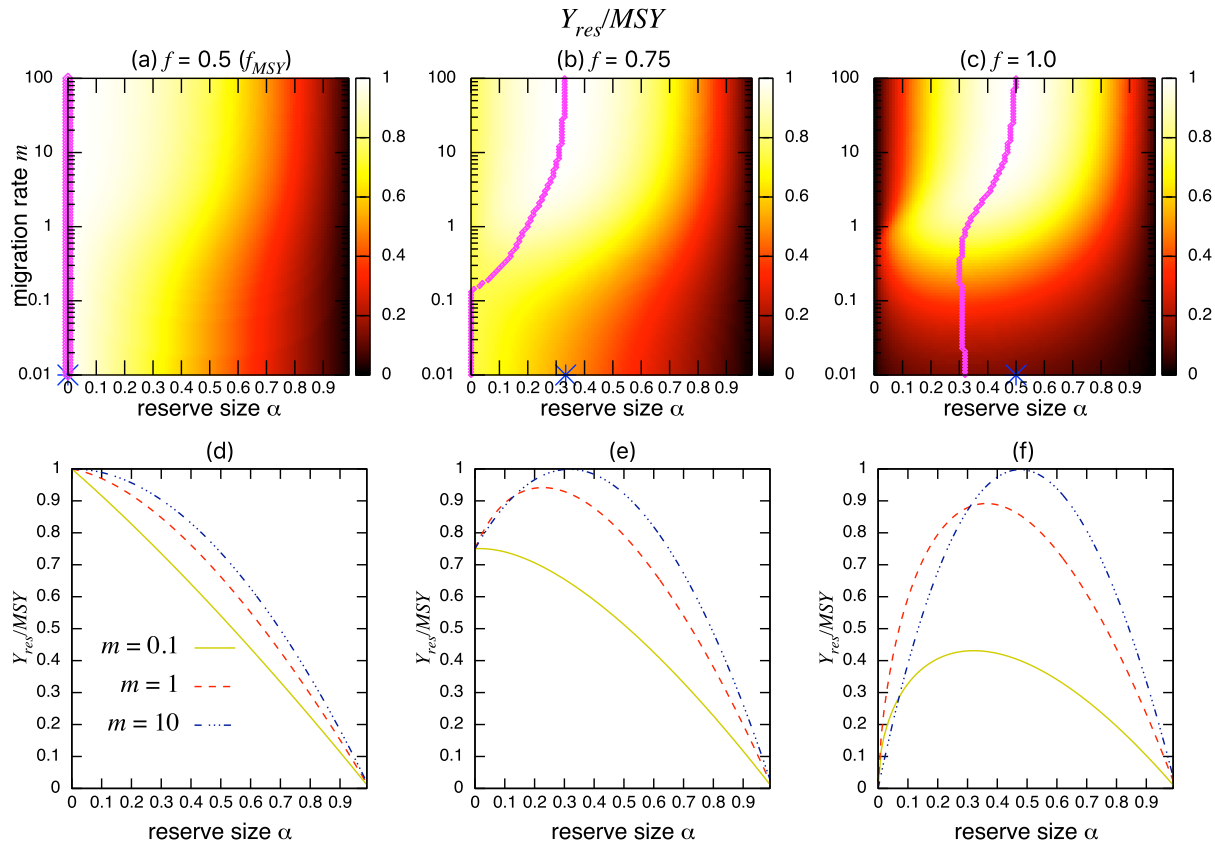

Figure 3: Effect of the marine reserve on the fishing yield across the reserve size α and migration rates m when the species migration is density independent. (Top) the normalized fishing yield (Y_{res}/MSY) and optimal reserve size α^* (magenta points (color online)). Lighter color in the heat map indicates larger value in Y_{res}/MSY. Optimal reserve size predicted by the aggregated model Eq. (6), α^{AG*}, is also shown on x-axis (blue star (color online)). (Bottom) Slices of the heat map above at $m = 0.1$, 1, and 10. The fishing mortality f corresponds to the value shown the top panel. The parameter values used are $r = 1$, $K = 10$, and $s = 0$.

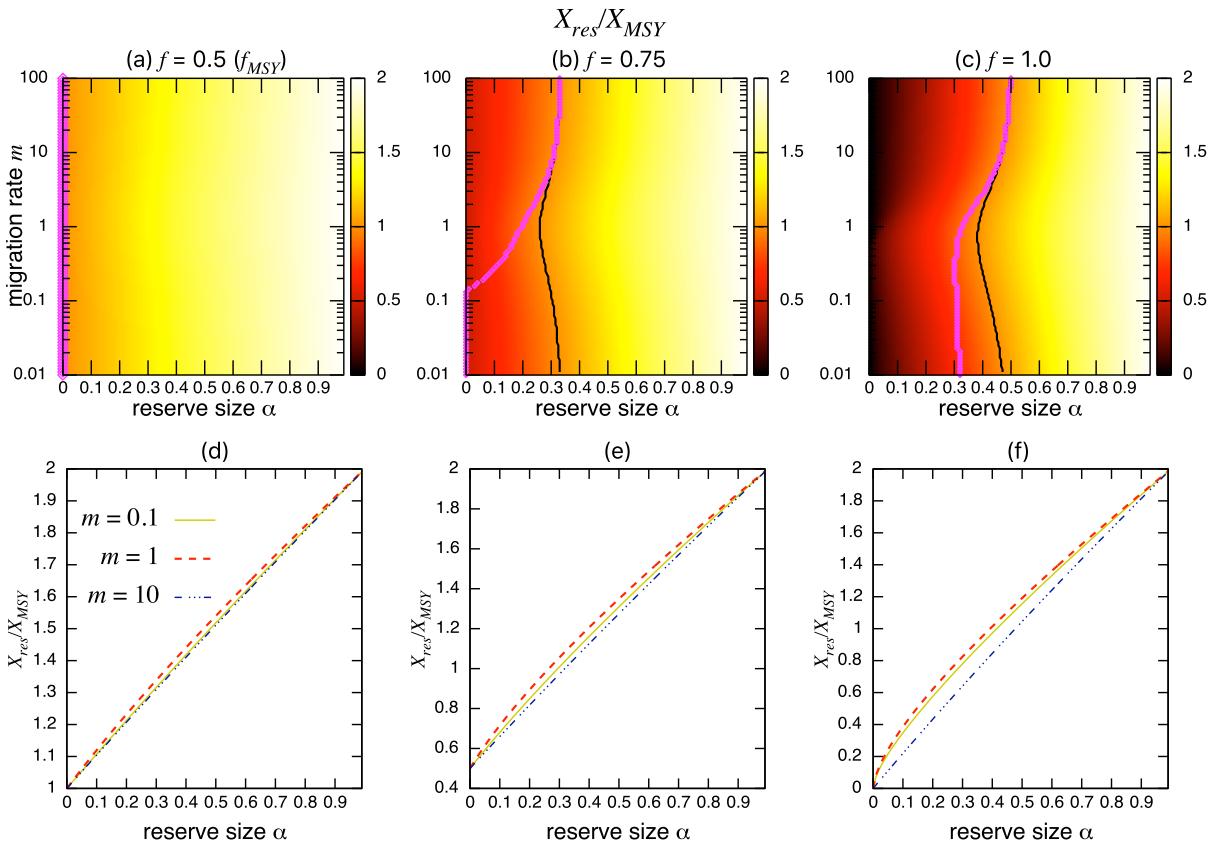

Figure 4: Effect of the marine reserve on the population size across the reserve size α and migration rates m when the species migration is density independent. (Top) the normalized population size (X_{res}/X_{MSY}) and optimal reserve size α^* (magenta points (color online)). Lighter color in the heat map indicates larger value in X_{res}/X_{MSY}. Black line represents the point where $X_{res}/X_{MSY} = 1$. (Bottom) Slices of the heat map above at $m = 0.1$, 1, and 10. The fishing mortality f corresponds to the value shown the top panel. The parameter values used are the same as in Fig. 3.

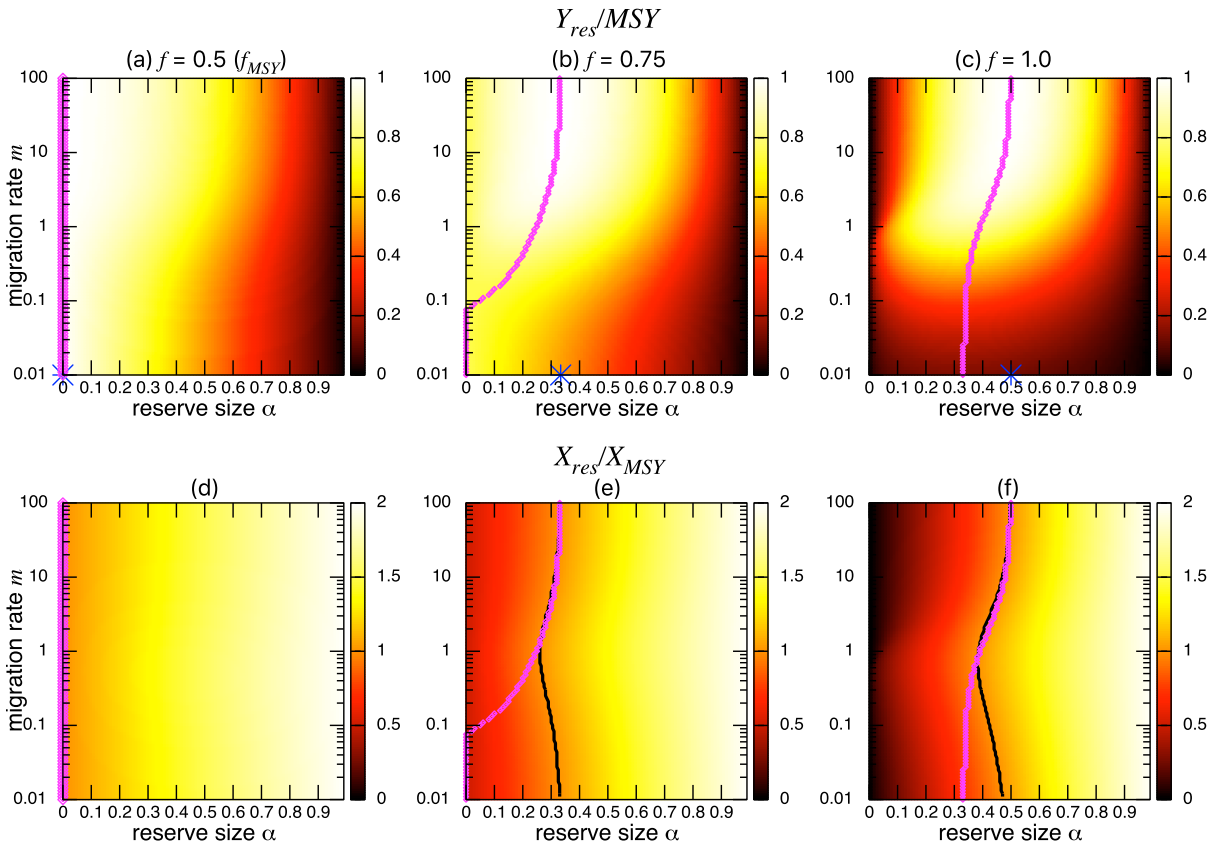

Figure 5: Effect of the marine reserve on the fishing yield and population size across the reserve size α and migration rates m when the species migration is positively density dependent ($s = 1$). (Top) the normalized fishing yield (Y_{res}/MSY). Optimal reserve size predicted by the aggregated model Eq. (6), α^{AG*}, is also shown on x-axis (blue star (color online)). (Bottom) the normalized population size (X_{res}/X_{MSY}). Black line represents the point where $X_{res}/X_{MSY} = 1$, and the magenta points (color online) show the optimal reserve size α^*. The other parameter values used are the same as in Fig. 3.

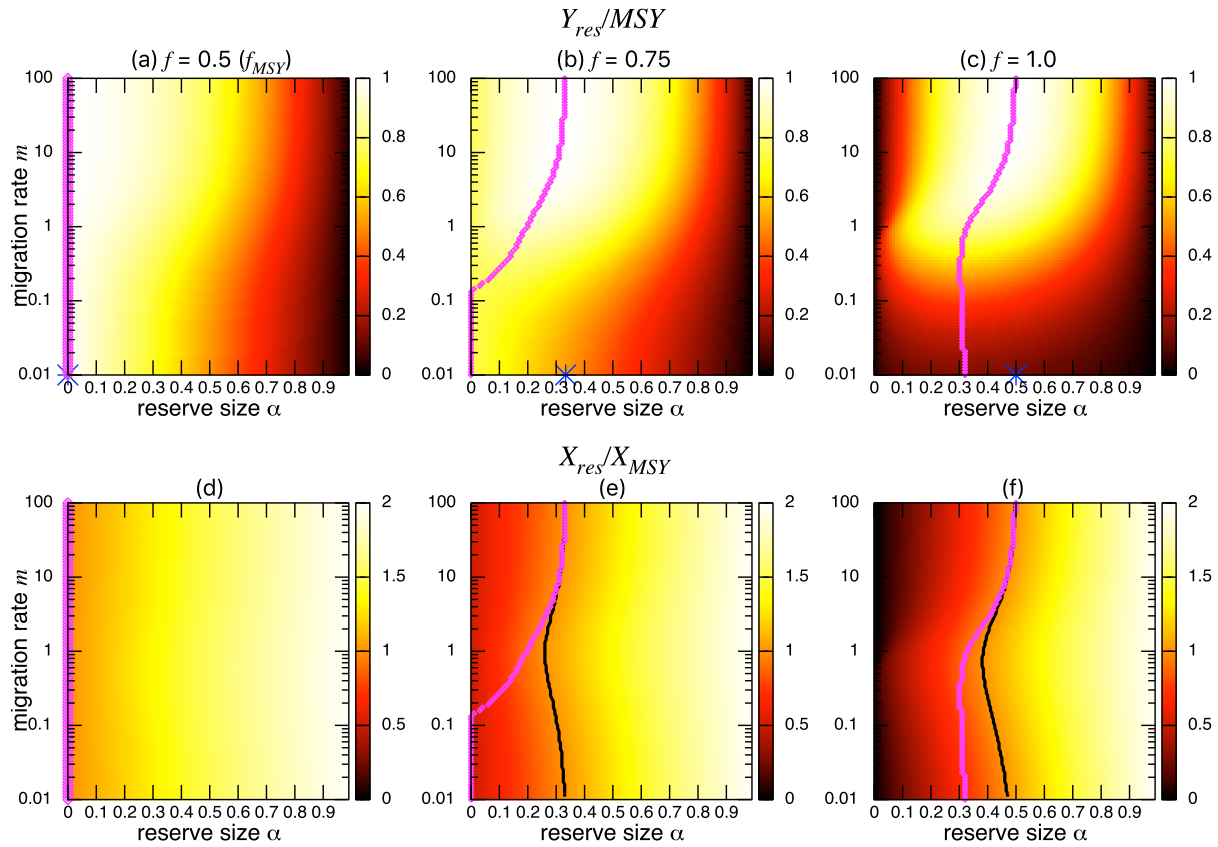

Figure 6: Effect of the marine reserve on the fishing yield and population size across the reserve size α and migration rates m when the species migration is negatively density dependent ($s = -0.5$). (Top) the normalized fishing yield (Y_{res}/MSY). Optimal reserve size predicted by the aggregated model Eq. (6), α^{AG*}, is also shown on x-axis (blue star (color online)). (Bottom) the normalized population size (X_{res}/X_{MSY}). Black line represents the point where $X_{res}/X_{MSY} = 1$, and the magenta points (color online) show the optimal reserve size α^*. The other parameter values used are the same as in Fig. 3.

4 Discussion

The effect of a marine reserve on harvesting is a crucial consideration as creating a marine reserve in the existing fishing ground can reduce fishing opportunities. By taking advantage of the simple mathematical model investigated, we demonstrated some important theoretical predictions to stipulate an optimal size of the marine reserve to maximize the fishing yield along with the total population size, a measure of conservation benefit. Our numerical simulations also examined various migration rates and modes and showed the theoretically predicted fishing yield gives an upper bound of the fishing yields.

The analysis of the aggregated model, describing the situation where the species migra-

tion rate is sufficiently large, suggests that fishing mortality should be larger than f_{MSY} for a marine reserve to improve the fishing yield (Fig. 2). Therefore, marine reserves do not deliver further fisheries benefit to sustainably managed fisheries below the MSY level. This confirms the finding of previous studies [21, 30, 31] under different modeling frameworks as mentioned in Introduction, suggesting generic characteristics of the marine reserve management. If a marine reserve replaces a certain fraction of fishing ground, fishing mortality should be increased by the factor inversely proportional to the fraction of the fishing ground. In practice, this corresponds to the situation where all fishermen remain in the contracted fishing ground after the reserve implementation. Under these conditions, the fishing yields becomes as large as MSY, as the previously reported result [7, 22]. Our results suggest that the optimal reserve fraction spans $\alpha^* \in (0, 1)$, and the optimal reserve fraction approaches to 1 as the fishing mortality becomes sufficiently large. This contrasts with previous studies where often a certain fraction of marine reserves are suggested to increase fishing yields (e.g., about 30% [12] or $20\% - 50\%$ [20] of the concerned region). Our numerical results suggest that these theoretical predictions from the aggregated model give the upper boundary of the harvesting. That is, the maximum harvest under the management with a marine reserve is achieved when the species migration rate becomes sufficiently large ($m \gg 1$). This indicates that the reduced fishing ground can be compensated by increasing the fishing mortality when there is sufficient species exchange between a marine reserve and fishing ground. However, the intensified fishing mortality to achieve the maximum fishing yield given a migration rate m often leads to a smaller total population than the MSY: $X_{res}/X_{MSY} < 1$, except for the case $m \gg 1$ where $X_{res}/X_{MSY} = 1$. On the other hand, the model shows the larger population size at an intermediate migration rate (Fig. 4b and c), representing the underlying tradeoff between fishing yield and population size (i.e., conservation benefit). Previous studies also showed that marine reserves may provide larger conservation benefits, such as a larger population recovery and reproductive capacity, at relatively low and moderate migration rate [8, 18, 41]. We also found these are relatively general outcomes under different migration modes (i.e., random or positively/negatively density-dependent migration). Moreover, a high migration rate vanishes the effect of different migration modes, and the fishing yields and population sizes converge to the same value at a large limit of the migration rate.

Our finding that the high migration rate ($m \gg 1$) produces the highest fishing yield implies a close relevance to the results in Neubert [29] where the optimal number of marine reserves to maximize the fishing yield can become infinitely many in a finite length of the one-dimensional space. Namely, placing infinitely many marine reserves in a finite space causes high population exchanges between reserves and non-reserve sites, and it may lead to the high migration rate ($m \gg 1$) in our model. It also suggests that the migration rate can be controlled by the configuration of marine reserves in space, and highlight the importance of the spatial scaling of management. Previously, Takashina and Baskett [39] demonstrated that the management unit scale is decomposed from the spatial scale in which biological processes operate. They showed that the fisheries management with a finer management unit scale results in a larger fishing yields than the management with a larger management scale since the former can realize a fine-tuned allocation of fishing efforts across management units. Fine-

tuned fishing activities across fishing grounds give higher flexibility in management decision making than our two-patch model, where we can assign only a single fishing mortality rate. Hence, the consideration of the migration rate as a function of the management unit scale may offer us a more flexible way to mitigate the underlying management tradeoff, and further investigation will be necessary.

The prediction of the equivalence in MSY and the yield from the management with a marine reserve has been revised by proceeding studies where the management with marine reserve shown to produce a larger fishing yield than MSY. For example, Gaylord et al. [13] and Ralston and O'Farrell [31] attributed the excess of yields to spatial structures of the model and post-dispersal density-dependent recruitment of larvae, and De Leo and Micheli [11] demonstrated a highly complex spatially-explicit and stage-structured stochastic model produces improved fishing yields. White and Kendall [45] claimed that the model complexity is not responsible for this result, and they demonstrated that only the effect of post-dispersal density-dependent in population dynamics induces the excess of fishing yields. On the other hand, our simple mathematical model does not show such excess, but numerical calculations suggest that an analytically derived optimal value corresponding to MSY. The lack of detailed spatial structures, stage/age-structure, and/or post-dispersal density-dependent recruitment, as in the above examples, may attribute this contrasting result. Particularly, the species migration and larval dispersal cause a rather different population mixing pattern. That is, the post-dispersal density-dependent recruitment causes a spontaneous reduction of the larvae number at recruitment, and it is often assumed to occur at a discrete-time (i.e., seasonal breeding cycle) as in the examples above [11, 13, 31, 45]. Contrary to these models, our continuous-time model regulates the population size by a density-dependent effect on the adult population dynamics where population reduction, given a larger population size than the carrying capacity, occurs gradually, and migrations of adult individuals between patches happen across the year. Furthermore, these movement patterns across space operate at different spatial scales, and influence on fishing activities also differ [18]. In marine environments connected by larval dispersals, less mobile species are more likely to increase fishing yields than highly mobile species. Namely, sessile species in reserves tend to stay in reserve longer and, hence, receive the larger benefit of reserves and can provide larger recruitment to fishing ground [24, 47]. On the other hand, highly mobile adult movement causes frequent population exchanges between reserves and fishing grounds, and they are more vulnerable to fishing activities than sessile species, leading to a higher fishing yield than a species with less mobile adult movement. Provided that the optimal yield in our aggregated model may be the upper bound in our two-patch model, our model can play as a basic model to assess the effect of, for instance, stage/age-structure, density-dependent larval recruitment, and more complex fishing regulations under different levels of spillover. For example, size/age-based regulation is prevalent in fisheries management, and its explicit consideration with various species migration scenarios further improves our understanding of the optimal size of marine reserves.

As described in Introduction, the optimal size of marine reserves in the paper is about the optimal fishing yield. However, optimizing harvest is merely one aspect of the management

with marine reserves, and there are a multitude of benefits of management and ecosystems, including enhancing ecological resilience [5, 41], and optimal profit [36], promoting biodiversity [34] and genetic diversity [6], and mitigating impacts of climatic change [17, 32] and catastrophic events [46]. Consequently, these form multiple tradeoffs of the management with marine reserves, and one needs to mitigate or even eliminate underlying tradeoffs to establish an optimal marine reserve [12, 27]. Recently, White et al [46] demonstrated that removal of the tradeoff between fishing and conservation benefits is mediated by a catastrophic event, suggesting that evaluating adequate components of management goals facilitates the decision making. However, the management under an optimal reserve size α^* to achieve an optimal fishing yield is still a useful baseline to assess the strength of multiple tradeoffs. Integrative discussion of multiple management objects to mitigate the tradeoffs will promote an effective management decision making.

Acknowledgements

NT was financially supported by Grant-in-Aid for the Japan Society for the Promotion of Science Fellows. I thank the two anonymous reviewers for their thoughtful comments.

References

[1] R. A. Abesamis and G. R. Russ. Density-dependent spillover from a marine reserve: Long-term evidence. *Ecol. Appl.*, 15:1798–1812, 2005.

[2] G. R. Almany, S. R. Connolly, D. D. Heath, J. D. Hogan, G. P. Jones, L. J. McCook, M. Mills, R. L. Pressey, and D. H. Williamson. Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs*, 28:339–351, 2009.

[3] P. Amarasekare. The role of density-dependent dispersal in source-sink dynamics. *J. Theor. Biol.*, 226:159–168, 2004.

[4] P. Auger, R. de La Parra, and J. Poggiale. Aggregation methods in dynamical systems and applications in population and community dynamics. *Phys. Life Rev.*, 5:79–105, 2008.

[5] L. A. Barnett and M. L. Baskett. Marine reserves can enhance ecological resilience. *Ecol. Lett.*, 18:1301–1310, 2015.

[6] M. L. Baskett and L. A. Barnett. The Ecological and Evolutionary Consequences of Marine Reserves. *Annu. Rev. Ecol. Evol. Syst.*, 46:49–73, 2015.

[7] M. Bensenane, A. Moussaoui, and P. Auger. On the Optimal Size of Marine Reserves. *Acta Biotheor.*, 61:109–118, 2013.

[8] R. E. Blyth-Skyrme, M. J. Kaiser, J. G. Hiddink, G. Edwards-Jones, and P. J. Hart. Conservation benefits of temperate marine protected areas: Variation among fish species. *Conserv. Biol.*, 20:811–820, 2006.

[9] Y. M. Bozec, S. O'Farrell, J. H. Bruggemann, B. E. Luckhurst, and P. J. Mumby. Tradeoffs between fisheries harvest and the resilience of coral reefs. *Proc. Natl. Acad. Sci. U. S. A.*, 113:4536–4541, 2016.

[10] L. B. Crowder, S. J. Lyman, W. F. Figueira, and J. Priddy. Source-sink population dynamics and the problem of siting marine reserves. *Bull. Mar. Sci.*, 66:799–820, 2000.

[11] G. A. De Leo and F. Micheli. The good, the bad and the ugly of marine reserves for fishery yields. *Philos. Trans. R. Soc. B Biol. Sci.*, 370:20140276, 2015.

[12] S. D. Gaines, C. White, M. H. Carr, and S. R. Palumbi. Designing marine reserve networks for both conservation and fisheries management. *Proc. Natl. Acad. Sci. U. S. A.*, 107:18286–18293, 2010.

[13] B. Gaylord, S. D. Gaines, D. A. Siegel, and M. H. Carr. Marine reserves exploit population structure and life history in potentially improving fisheries yields. *Ecol. Appl.*, 15:2180–2191, 2005.

[14] B. Ghosh, D. Pal, T. K. Kar, and J. C. Valverde. Biological conservation through marine protected areas in the presence of alternative stable states. *Math. Biosci.*, 286:49–57, 2017.

[15] R. Goñi, A. Quetglas, and O. Reñones. Spillover of spiny lobsters Palinurus elephas from a marine reserve to an adjoining fishery. *Mar. Ecol. Prog. Ser.*, 308:207–219, 2006.

[16] H. S. Gordon. The economic theory of a common-property resource: the fishery. *J. Polit. Econ.*, 62:124–142, 1954.

[17] A. L. Green, L. Fernandes, G. Almany, R. Abesamis, E. McLeod, P. M. Aliño, A. T. White, R. Salm, J. Tanzer, and R. L. Pressey. Designing Marine Reserves for Fisheries Management, Biodiversity Conservation, and Climate Change Adaptation. *Coast. Manag.*, 42:143–159, 2014.

[18] A. Gruss, D. M. Kaplan, S. Guenette, C. M. Roberts, and L. W. Botsford. Consequences of adult and juvenile movement for marine protected areas. *Biol. Conserv.*, 144:692–702, 2011.

[19] B. S. Halpern, S. E. Lester, and J. B. Kellner. Spillover from marine reserves and the replenishment of fished stocks. *Environ. Conserv.*, 36:268–276, 2009.

[20] B. S. Halpern and R. R. Warner. Matching marine reserve design to reserve objectives. *Proc. R. Soc. B Biol. Sci.*, 270:1871–1878, 2003.

[21] D. R. Hart. When do marine reserves increase fishery yield? *Can. J. Fish. Aquat. Sci.*, 63:1445–1449, 2006.

[22] A. Hastings and L. Botsford. Equivalence in yield from marine reserves and traditional fisheries management. *Science*, 5419:1537–1538, 1999.

[23] A. Hastings, S. D. Gaines, and C. Costello. Marine reserves solve an important bycatch problem in fisheries. *Proc. Natl. Acad. Sci. U. S. A.*, 114:8927–8934, 2017.

[24] D. S. Holland and R. J. Brazee. Marine Reserves for Fisheries Management. *Mar. Resour. Econ.*, 11:157–171, 1996.

[25] Y. Iwasa and V. Andreasen. Aggregation in model ecosystems. I. Perfect aggregation. *Ecol. Modell.*, 37:287–302, 1987.

[26] J. Kellner, I. Tetreault, and S. Gaines. Fishing the line near marine reserves in single and multispecies fisheries. *Ecol. Appl.*, 17:1039–1054, 2007.

[27] C. J. Klein, V. J. Tulloch, B. S. Halpern, K. A. Selkoe, M. E. Watts, C. Steinback, A. Scholz, and H. P. Possingham. Tradeoffs in marine reserve design: Habitat condition, representation, and socioeconomic costs. *Conserv. Lett.*, 6:324–332, 2013.

[28] E. A. Moffitt, L. W. Botsford, D. M. Kaplan, and M. R. O'Farrell. Marine reserve networks for species that move within a home range. *Ecol. Appl.*, 19:1835–1847, 2009.

[29] M. Neubert. Marine reserves and optimal harvesting. *Ecol. Lett.*, 6:843–849, 2003.

[30] J. C. Pezzey, C. M. Roberts, and B. T. Urdal. A simple bioeconomic model of a marine reserve. *Ecol. Econ.*, 33:77–91, 2000.

[31] S. Ralston and M. R. O'Farrell. Spatial variation in fishing intensity and its effect on yield. *Can. J. Fish. Aquat. Sci.*, 65:588–599, 2008.

[32] C. M. Roberts, B. C. O'Leary, D. J. McCauley, P. M. Cury, C. M. Duarte, J. Lubchenco, D. Pauly, A. Sáenz-Arroyo, U. R. Sumaila, R. W. Wilson, B. Worm, and J. C. Castilla. Marine reserves can mitigate and promote adaptation to climate change. *Proc. Natl. Acad. Sci. U. S. A.*, 114:6167–6175, jun 2017.

[33] R. Rosenberg, H. C. Nilsson, K. Hollertz, and B. Hellman. Density-dependent migration in an Amphiura filiformis (Amphiuridae, Echinodermata) infaunal population. *Mar. Ecol. Prog. Ser.*, 159:121–131, 1997.

[34] G. R. Russ and A. C. Alcala. Enhanced biodiversity beyond marine reserve boundaries: The cup spillith over. *Ecol. Appl.*, 21:241–250, 2011.

[35] E. Sala and S. Giakoumi. No-take marine reserves are the most effective protected areas in the ocean. *ICES J. Mar. Sci.*, 75:1166–1168, 2018.

[36] J. N. Sanchirico, U. Malvadkar, A. Hastings, and J. E. Wilen. When are no-take zones an economically optimal fishery management strategy? *Ecol. Appl.*, 16:1643–1659, 2006.

[37] M. Schaefer. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. *Bull. Inter-American Trop. Tuna Comm.*, 1:27–56, 1954.

[38] N. Takashina. Simple rules for establishment of effective marine protected areas in an age-structured metapopulation. *J. Theor. Biol.*, 391:88–94, 2016.

[39] N. Takashina and M. L. Baskett. Exploring the effect of the spatial scale of fishery management. *J. Theor. Biol.*, 390:14–22, 2016.

[40] N. Takashina, J. H. Lee, and H. P. Possingham. Effect of marine reserve establishment on non-cooperative fisheries management. *Ecol. Modell.*, 360:336–342, 2017.

[41] N. Takashina and A. Mougi. Effects of marine protected areas on overfished fishing stocks with multiple stable states. *J. Theor. Biol.*, 341:64–70, 2014.

[42] N. Takashina and A. Mougi. Maximum sustainable yields from a spatially-explicit harvest model. *J. Theor. Biol.*, 383:87–92, 2015.

[43] N. Takashina, A. Mougi, and Y. Iwasa. Paradox of marine protected areas: suppression of fishing may cause species loss. *Popul. Ecol.*, 54:475–485, 2012.

[44] C. White and C. Costello. Close the High Seas to Fishing? *PLoS Biol.*, 12:e1001826, 2014.

[45] C. White and B. E. Kendall. A reassessment of equivalence in yield from marine reserves and traditional fisheries managament. *Oikos*, 116:2039–2043, 2007.

[46] E. R. White, M. L. Baskett, and A. Hastings. Catastrophes, connectivity, and Allee effects in the design of marine reserve networks. *bioRxiv*, page 750448, 2019.

[47] J. W. White, L. W. Botsford, E. A. Moffitt, and D. T. Fischer. Decision analysis for designing marine protected areas for multiple species with uncertain fishery status. *Ecol. Appl.*, 20:1523–1541, 2010.