

Contents lists available at ScienceDirect

# Journal of Theoretical Biology



journal homepage: www.elsevier.com/locate/yjtbi

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## HIGHLIGHTS

- We investigated effects of MPAs on ecosystems with multiple stable states (MSS).
- Transported fishing efforts from the MPA may hamper recovery of fishing stocks.
- The transported efforts may also have the effect to weaken ecological resilience.
- Sedentary species is not feasible target of MPAs in an ecosystem with MSS.

## ARTICLE INFO

Article history: Received 29 March 2013 Received in revised form 13 August 2013 Accepted 18 September 2013 Available online 29 September 2013

Keywords: MPAs Depleted fishing stocks Regime shift Ecological resilience

## ABSTRACT

Marine protected areas (MPAs) have attracted much attention as a tool for sustainable fisheries management, restoring depleted fisheries stocks and maintaining ecosystems. However, even with total exclusion of fishing effort, depleted stocks sometimes show little or no recovery over a long time period. Here, using a mathematical model, we show that multiple stable states may hold the key to understanding the tendency for fisheries stocks to recover because of MPAs. We find that MPAs can have either a positive effect or almost no effect on the recovery of depleted fishing stocks, depending on the fish migration patterns and the fishing policies. MPAs also reinforce ecological resilience, particularly for migratory species. In contrast to previous reports, our results show that MPAs have small or sometimes negative effects on the recovery of sedentary species. Unsuitable MPA planning might result in low effectiveness or even deterioration of the existing condition.

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## 1. Introduction

In recent years, the conditions of more than 30% of fishing stocks have been described as overexploited, depleted or recovering (FAO, 2012). Marine protected areas (MPAs) have attracted much attention as a tool for sustainable fisheries management, restoring depleted fishing stocks and maintaining ecosystems (Hastings and Botsford, 1999; Palumbi, 2001; Roberts et al., 2005; White et al., 2011). A number of MPAs have been established around the world and have restored depleted fishing stocks (Lester et al., 2009; Molloy et al., 2009; Stockwell et al., 2009; Aburto-Oropeza et al., 2011; Russ and Angel, 2011). However, depleted fishing stocks sometimes show little or no recovery over a long time period, despite the reduction or exclusion of fishing effort from the protected area (Hutchings, 2000).

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This suggests that the creation of no-take marine reserves or MPAs might sometimes have no effect on the recovery of fishing stocks. One hypothesis to explain this lack of recovery is the existence of multiple stable states.

In natural environments, both terrestrial and marine, ecosystems often undergo catastrophic changes and the existence of multiple stable states has been asserted (May, 1977; Ludwig et al., 1978; Scheffer et al., 2001; deYoung et al., 2008). Historically, collapses of a number of fishing stocks due to the failure of fisheries management have been reported (e.g., Hutchings and Reynolds, 2004). When such damaged ecosystems recover, they often show the following characteristics of multiple stable states: (1) they exhibit varying degrees of hysteresis: the trajectories of recovery are different from that of decline (Hughes et al., 2005); (2) sustaining a resilient ecosystem is easier than recovering it after phase shift has occurred (Hughes et al., 2005; Beisner et al., 2003). In spite of recognizing the inherent patterns of multiple stable states in marine environments, many studies on MPAs have ignored the effects of multiple stable states. Consideration of multiple stable states provides us a new perspective to the effects of MPAs on depleted fishing stocks.

<sup>\*</sup>Statement of authorship: NT performed the model construction, simulation, and wrote the first draft. AM performed also the model construction, and both authors contributed substantially to revisions.

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Here, using a mathematical model, we show the effects of MPAs on depleted fishing stocks having multiple stable states. In the following analysis, the term MPA is used referring to a no-take marine reserve where all human uses contributing ecosystem impacts are not allowed. First, we examine the effects of MPAs on the recovery of the equilibrium population size of the depleted fishing stock. Population size is the most common measure in fishery management, providing evidence for the efficacy of MPAs. Second, we examine the changes of ecological resilience, defined as the size of the basin of attraction or the width of the stability basin in a common ball-in-cup diagram (Peterson et al., 1998). This measure is not commonly used in fishery management, but it might provide a useful insight into how to manage a fishing stock with multiple stable states. We show that the introduction of the MPA affects the restoration of the depleted fishing stocks and can enhance the ecological resilience. We also show that the degree of these positive effects of MPAs varies widely depending on the migration characteristics of the target species and the fishing policies. The results provide us with new insights as to how the MPA works in the management of depleted stocks and in resilience-based ecosystem management (Hughes et al., 2005; Briske et al., 2008; Ling et al., 2009).

## 2. Methods

### 2.1. Population dynamics

To explore the efficacy of MPAs in ecosystems with multiple stable states, we use the canonical model giving multiple stable states, which is often applied to marine systems (e.g., May, 1977; Ludwig et al., 1978; Steele and Henderson, 1984):

$$\frac{dX}{dt} = rX\left(1 - \frac{X}{K}\right) - \frac{aPX^2}{b^2 + X^2} \tag{1}$$

where X is the population density, r is the intrinsic growth rate, K is the carrying capacity, a is the predator's consumption rate, P is the constant predator density, and b is the half-saturation level of predation. By introducing a linear harvest term, which is commonly used in fisheries models, Eq. (1) becomes

$$\frac{dX}{dt} = rX\left(1 - \frac{X}{K}\right) - \frac{aPX^2}{b^2 + X^2} - qEX$$
(2)

where *q* is the catchability coefficient and *E* is the fishing effort. *E* is typically specified as the number of vessels actively fishing (Clark 1990). This model has been used to evaluate the effects of alternative stable states in fisheries and is known to have lower stable state  $X_L^*$  and upper stable state  $X_U^*$  (Spencer and Collie 1996; Steele and Beet 2003).

When the MPA is introduced, the ecosystem would be separated into two patches: the fishing ground and the protected area (MPA; Fig. 1). Hence, we use a two-patch model to explore the effects of MPAs (e.g., Steele and Beet, 2003; Micheli et al., 2004; Ami et al., 2005; Greenville and MacAulay, 2006; Kar and Matsuda, 2008; West et al., 2009; Takashina et al., 2012). When the MPA is



Fig. 1. Schematic description of the model.

considered, the model is described by the following two equations (see Appendix A for more details):

$$\frac{dX_1}{dt} = rX_1 \left( 1 - \frac{X_1}{K} \right) - \frac{aPX_1^2}{b^2 + X_1^2} - \frac{qEX_1}{1 - \sigma R} + mR \left( \left( \frac{X_2}{K} \right)^s X_2 - \left( \frac{X_1}{K} \right)^s X_1 \right)$$
(3a)  
$$\frac{dX_2}{dt} = rX_2 \left( 1 - \frac{X_2}{K} \right) - \frac{aPX_2^2}{b^2 + X_2^2} + m(1 - R) \left( \left( \frac{X_1}{K} \right)^s X_1 - \left( \frac{X_2}{K} \right)^s X_2 \right)$$

(3b)

where  $X_1$  and  $X_2$  are the population density in the fishing ground and the MPA, respectively. *m* is the migration rate. *R* is the fraction of the MPA and 1 - R is the fraction of the fishing ground.  $\sigma$  is the effort redistribution coefficient which represents the intensity of fishing effort transfer into the fishing ground due to the creation of the MPA. When  $\sigma = 0$ , the fishing effort over the fishing ground does not change, with or without the MPA. In other words, the number of vessels actively fishing in the fishing ground per unit area is same as before the MPA creation (CEP: constant effort policy). When  $0 < \sigma < 1$ , the fishing effort increases with the increasing fraction of MPA. This corresponds to a situation where fishing vessels previously exerted in the pre-MPA are redistributed to the fishing ground and as a result the number of vessels actively fishing in the fishing ground per unit area is increased after the establishment of the MPA (ERP: effort redistribution policy), at the rate of inverse  $1 - \sigma R$ .

The last terms on the right hand side of Eqs. (3a) and (3b) represent migration between two patches involving the density effect defined by Amarasekare (2004). s is the strength of densitydependence of migration. When s=0, the migration is random. This case corresponds to the random migration defined, for example, by Takashina et al. (2012). The first and second terms in the square brackets of Eq. (3a) represent the immigration from the patch 2 and the emigration to the patch 2, respectively (Amarasekare 2004). When s > 0, emigration increases with population density at an accelerating rate (density-dependent migration; DM). This pattern of migration has been documented in a number of marine organisms, including fish and echinoderms (Rosenberg et al., 1997; Abesamis and Russ. 2005: Kellner et al., 2008). When -1 < s < 0 emigration increases with population density at a decelerating rate (negative density-dependent migration; NDM). This type of migration may occur as a result of the Allee (1931) effect.

To reduce the number of parameters, we use the following nondimensional form of the equations (Murray, 2002) (see Appendix A):

$$\frac{d\hat{x}_1}{d\tau} = \hat{x}_1(1-\hat{x}_1) - \frac{\beta_2 \hat{x}_1^2}{\beta_1^2 + \hat{x}_1^2} - \frac{\beta_3 \hat{x}_1}{1 - \sigma R} + \beta_4 R(\hat{x}_2^{s+1} - \hat{x}_1^{s+1})$$
(4a)

$$\frac{d\hat{x}_2}{d\tau} = \hat{x}_2 \left(1 - \hat{x}_2\right) - \frac{\beta_2 \hat{x}_2^2}{\beta_1^2 + \hat{x}_2^2} + \beta_4 (1 - R)(\hat{x}_1^{s+1} - \hat{x}_2^{s+1})$$
(4b)

where,  $\hat{x}_i$  (i=1, 2) is the non-dimensional parameter of  $X_i$ , and  $\tau$  is the non-dimensional time metric scaled by intrinsic growth rate (see Appendix A). Here, we assume that multiple stable states are introduced due to the fishing activity. That is, multiple stable states do not exist when the MPA is absent (R=0). We set  $\beta_1$ =0.1 (Spencer and Collie, 1996; Steele and Beet, 2003),  $\beta_2$ =0.17, and  $\beta_3$ =0.15. These parameter values are chosen so as to have multiple stable states in our model, in the absence of MPA (R=0).

## 2.2. Ecological resilience

In the presence of multiple stable states, we can consider the ecological resilience, which is the 2-dimensional extension of the ecological resilience defined by Peterson et al. (1998): the length of basin of attraction. Here we define ecological resilience in a 2D plane as  $\alpha_{R,80\%}/\alpha_R$ , where  $\alpha_R$  is an area of a phase plane of Eqs. (4a) and (4b)

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