Journal of Theoretical Biology ∎ (∎∎∎∎) ∎∎∎–∎∎∎

Contents lists available at ScienceDirect

Journal of Theoretical Biology

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

Maximum sustainable yields from a spatially-explicit harvest model

Nao Takashina [a,*], Akihiko Mougi [b]

[a] Department of Biology, Faculty of Sciences, Kyushu University, 6–10-1, Hakozaki, Fukuoka, 812-8581, Japan
[b] Department of Biological Science, Faculty of Life and Environmental Science, Shimane University, Nishikawatsu-cho 1060, Matsue 690-8504, Japan

HIGHLIGHTS

- Spatially-generalized harvest model is developed.
- Each patch in the model is characterized by the area and habitat quality.
- Integrating spatial structure may decrease the MSY value.
- The degree of the decline is calculated analytically.
- An easy method to estimate the degree of overestimation is provided.

ARTICLE INFO

Article history:
Received 29 April 2015
Received in revised form
23 July 2015
Accepted 26 July 2015

Keywords:
Maximum sustainable yields
Resource management
Schaefer model
Spatially-explicit model

ABSTRACT

Spatial heterogeneity plays an important role in complex ecosystem dynamics, and therefore is also an important consideration in sustainable resource management. However, little is known about how spatial effects can influence management targets derived from a non-spatial harvest model. Here, we extended the Schaefer model, a conventional non-spatial harvest model that is widely used in resource management, to a spatially-explicit harvest model by integrating environmental heterogeneities, as well as species exchange between patches. By comparing the maximum sustainable yields (MSY), one of the central management targets in resource management, obtained from the spatially extended model with that of the conventional model, we examined the effect of spatial heterogeneity. When spatial heterogeneity exists, we found that the Schaefer model tends to overestimate the MSY, implying potential for causing overharvesting. In addition, by assuming a well-mixed population in the heterogeneous environment, we showed analytically that the Schaefer model always overestimate the MSY, regardless of the number of patches existing. The degree of overestimation becomes significant when spatial heterogeneity is marked. Collectively, these results highlight the importance of integrating the spatial structure to conduct sustainable resource management.

1. Introduction

Diverse ranges of environments are characterized by spatial heterogeneity. Ecologists recognize that this heterogeneity plays a critical role in the complex dynamics of ecosystem (Hanski, 1998; Levin, 1992), and also it is practically an important consideration in ecosystem management (Plotkin and Muller-Landau, 2002). The use of spatially explicit approaches to the ecosystem management are increasing rapidly in response to the recent trends to involve reserves in terrestrial as well as marine ecosystem management (Baskett and Weitz, 2007; Lundberg and Jonzén, 1999; Neubert, 2003; Sanchirico and Wilen, 1999; Takashina et al., 2012; White and Costello, 2011; White et al., 2010; Williams and Hastings, 2013). On the other hand, in many management exercises, including fisheries management (Clark, 1990; Walters et al., 2005) and terrestrial wildlife hunting (Ling and Milner-Gulland, 2008; Robinson and Redford, 1991), managers traditionally use the concept of maximum sustainable yield (MSY) without consideration of the spatial structure. This is likely because most harvesting theories, in which MSY has played a major role in sustainable resource uses, originated in commercial fisheries science (Gordon, 1954; Schaefer, 1954) where spatial heterogeneity was not considered until recently (Ling and Milner-Gulland, 2008). Therefore, this leaves us to question how integrating the spatial structure affects the management goals in the harvesting model.

Ling and Milner-Gulland (2008) used a static spatial harvesting model but also considered the effects of traveling costs, showing that MSY can be overestimated when these costs are not taken

* Correspondence to: Tropical Biosphere Research Center, University of the Ryukyus, 3422 Sesoko, Motobu, Okinawa 905-0227, Japan. Tel.: +81 980 47 2888; fax: +81 980 47 4919.
E-mail addresses: nao.takashina@gmail.com (N. Takashina), amougi@gmail.com (A. Mougi).

http://dx.doi.org/10.1016/j.jtbi.2015.07.028
0022-5193/© 2015 Published by Elsevier Ltd.

into account. Ying et al. (2011) discussed the risks of ignoring spatial structure in a 10-year simulation of fisheries management, showing that such an omission resulted in a high probability of fishing stocks off the coast of China being over exploited and/or suffering localized depletions. Both papers highlight the importance of explicitly considering spatial structure in mitigating the risks of overestimation or overexploitation with a specific setting in mind. Křivan and Jana (2015) discussed the effect of the dispersal on harvesting with the no-take marine reserve where the two regions (the fishing ground and reserve) are characterized by the proportional size of the concerned area. They showed numerically that the dispersal of the species could lead to the decline of the population abundance as well as the MSY.

In this study, we developed a general spatially-explicit model which is naturally extended by the conventional (non-spatial) harvest model, and therefore we can apply it to various resource managements. One of the conventional models used widely in resource management is the Schaefer model (Clark, 1990; Schaefer, 1954). In addition, this model is often used as a basis for more complex ecosystem models (Neubert, 2003). In light of this, it may be rational to extend the Schaefer model to include a spatial structure as the first step towards the spatial extension of harvest models.

In this paper, we examine the spatial effect on the MSY of a harvesting model by extending the Schaefer model to a spatially generalized model. We show that when spatial structure is not considered, this omission leads to an overestimation in MSY, implying potential for causing overharvesting by providing larger amount of harvestable population. We also discuss the conditions in which the overestimation becomes significant, and a way to apply our model to an actual management to predict degree of the overestimation.

2. Methods

2.1. MSY in the Schaefer model

One of the most basic harvest models is the Schaefer model, which can be described as:

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

where x is population abundance, r the per capita growth rate (per unit time), K is the carrying capacity of the environment and e is the harvest rate (per unit time). Using this equation, MSY is calculated to be equal to $rK/4$ and thus, when MSY is reached, population abundance is equal to $K/2$ (Gordon, 1954; Schaefer, 1954).

2.2. The spatially explicit harvest model

In this study, we considered a simple spatial generalization of the Schaefer model, hereafter referred to as the spatially explicit harvest model (SEH). One of the simplest ways to spatially extend a non-spatial model is to divide the area being considered into two patches with the area fractions α and $1-\alpha$, and each of these patches is assumed to have different habitat qualities K_1 and K_2 (per unit area). It is worth stressing that the carrying capacity K in Eq. (1) and these habitat qualities are not the same quantities due to the difference in their units. The carrying capacities in the SHE model are then the product of the area fraction and the habitat quality in the patch (Fig. 1), and therefore $K = \alpha K_1 + (1-\alpha)K_2$. The two patches are interconnected through the exchange of individuals from the two populations, an event that is represented by the exchange rate m, defined for each time period and each patch.

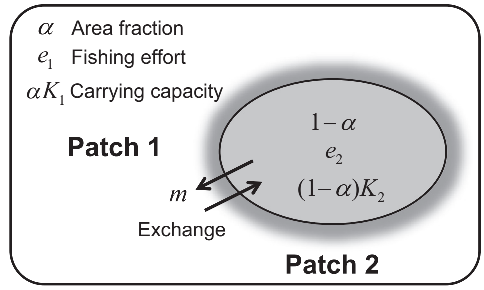

Fig. 1. Schematic description of the spatial-integrated Schaefer model. Environmental heterogeneities create two different patches in the concerned area. Two patches have different habitat qualities K_i ($i=1, 2$) and fractions of the area α, $1-\alpha$ and exchange of species connect with patches at rate m.

Therefore, the actual exchange rate between populations is proportional to the area of other patch and the population abundance x_i ($i=1, 2$) in the focal patch. We add the exchange terms to the Schaefer model (Eq. (1)) to obtain the two-patch SEH model:

$$\frac{dx_1}{dt} = rx_1\left(1-\frac{x_1}{\alpha K_1}\right) - e_1x_1 + m(\alpha x_2 - (1-\alpha)x_1), \tag{2a}$$

$$\frac{dx_2}{dt} = rx_2\left(1-\frac{x_2}{(1-\alpha)K_2}\right) - e_2x_2 + m((1-\alpha)x_1 - \alpha x_2). \tag{2b}$$

The subdivision of the area does not change r and managers can take different harvest rates e_i for each patch.

2.3. The Schaefer model versus the SEH model

To examine the effects of spatial differences on MSY we compared the MSYs calculated by both the Schaefer and SEH models. In the SEH model, the conventional MSY becomes $r(\alpha K_1 + (1-\alpha)K_2)/4$, noting that the K in Eq. (1) has been replaced by the total carrying capacity of the whole area. For simplicity, r was set at unity, but it does not change the ratio between the conventional MSY and the MSY in the SHE model because it does not appear in the ratio.

For the SEH model, it was possible to calculate two different MSY values depending on which management regime was applied. In the first regime (uMSY) harvest rates were assumed to be uniform for both patches (i.e., $e_1 = e_2$) whilst for the second regime (gMSY) harvest rates were altered in both patches with a view to reaching a global MSY that was defined as the MSY in the whole area.

In the following section, we examine the effect of space on MSY in cases where the two patches are isolated, connected through an intermediate exchange rate or well-mixed by a high exchange rate. For more general situations, we also considered an n-patch generalization of the SHE model for broader applications. We did not examine the population abundance at the MSY values, because the MSY in the Schaefer model is proportional to the population abundance at the MSY value and one may infer the spatial effect to the population abundance at the MSY.

3. Results

3.1. The two-patch SHE model

3.1.1. Isolated patches

When the two sections are isolated from each other (i.e., thus $m=0$ in Eqs. (2a) and (2b)), uMSY and gMSY are simply the sum of the MSY values calculated independently for each section. In this case, it is then clear that uMSY is equal to gMSY, and also that they