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Effects of animal dispersal on harvesting with protected areas

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HIGHLIGHTS

- Effect of dispersal on (marine) protected areas functioning is studied.
- Dispersal modes studied are either density independent, or density dependent and in direction of higher fitness.
- Density independent dispersal is either balanced, or unbalanced.
- Results show that dispersal influences both the maximum sustainable yield and population equilibrium abundance.
- Dispersal also decreases population abundance when compared with the same system without dispersal.
- Dilemma caused by creation of protected areas (i.e., increased population abundance vs. decreased profit) are dispersal dependent.

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ABSTRACT

Effects of density dependent as well as independent dispersal modes between a harvested patch and a protected area on the maximum sustainable yield and population abundance are studied. Without dispersal, the Gordon-Schaefer harvesting model predicts that as the protected area increases, population abundance increases too but the maximum sustainable yield (MSY) decreases. This article shows that dispersal can change this prediction. For density independent balanced and fast dispersal, neither the MSY, nor population abundance depends on the protected area. For fast and unbalanced dispersal both the MSY and equilibrium population abundance are unimodal functions of the protected area size. For density dependent dispersal which is in direction of increasing fitness predictions depend on whether individuals react to mortality risk in harvested patch. When animals disregard harvesting risk, the results are similar to the case of density independent and balanced dispersal. When animals do consider harvesting risk, the results are similar to the case without dispersal. The models considered also show that dispersal reduces beneficial effect of protected areas, because population abundance is smaller when compared with no dispersal case.

1. Introduction

Exploitation of renewable resources are commonly practiced in fishery, forestry and wildlife management. Extensive and unregulated harvesting of marine species leads to the depletion of several commercial fish stocks. Bioeconomic modeling (Clark, 1976) provides theoretical underpinnings for scientific management of renewable resources. One approach to prevent overexploitation is creation of protected areas where harvesting is prohibited. Protected areas should increase fish abundance and protect biodiversity and ecosystem structure (Beverton, 1953; Gordon, 1954). However, creation of protected areas leads to a dilemma, because the Gordon-Schaefer bioeconomic model (Clark, 1976) predicts reduction of the maximum sustainable yield (MSY). More sophisticated models suggest that optimal spatial management can increase both MSY as well as the resource standing stock (Neubert and Herrera, 2008). These models often assume that dispersal between patches is density independent (e.g., Takeuchi, 1996; Kar and Matsuda, 2008). However, it is known that density independent dispersal is not evolutionarily stable (Hastings, 1983) unless dispersal rates are balanced in the sense that patches are occupied up to their carrying capacity (McPeek and Holt, 1992; Holt and Barfield, 2001). Density dependent models of refuge use were also studied in the literature (e.g., Ives and Dobson, 1987; Sih, 1987; Ruxton, 1995; Křivan, 1998; Grüss et al., 2011; Křivan, 2013; Takashina and Mougi, 2014). These models reflect empirical observations that prey dispersal is a function of patch payoffs (Sih, 1980, 1986; Lima and Dill, 1990; Peacor and Werner, 2001; Brown and Kotler, 2004).

Fretwell and Lucas (1969) introduced the ideal free distribution (IFD) under which animals redistribute between patches so that all

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occupied patches have the same payoff that is larger than or equal to payoffs in unoccupied patches. Thus, only dispersal patterns that lead to the IFD can be evolutionarily stable (Cantrell et al., 2010, 2012). Cressman and Křivan (2006) proved that when patch payoffs are negatively density dependent, the IFD is an evolutionarily stable strategy of the habitat selection game (Křivan et al., 2008). The IFD assumes that individuals have a perfect knowledge of patch qualities and they are free to settle in any patch they want. Although these assumptions are not realistic under many circumstances, it is interesting that experimental and empirical work often predicts distributions that are close to the IFD (for a critical review see Kennedy and Gray, 1993). In particular, fish distributions have been observed to follow the IFD closely (e.g. Milinski, 1979; Berec et al., 2006; Haugen et al., 2006). Consequences of dispersal on refuge functioning was reviewed in Gerber et al. (2003) and Grüss et al. (2011). Both these reviews make clear

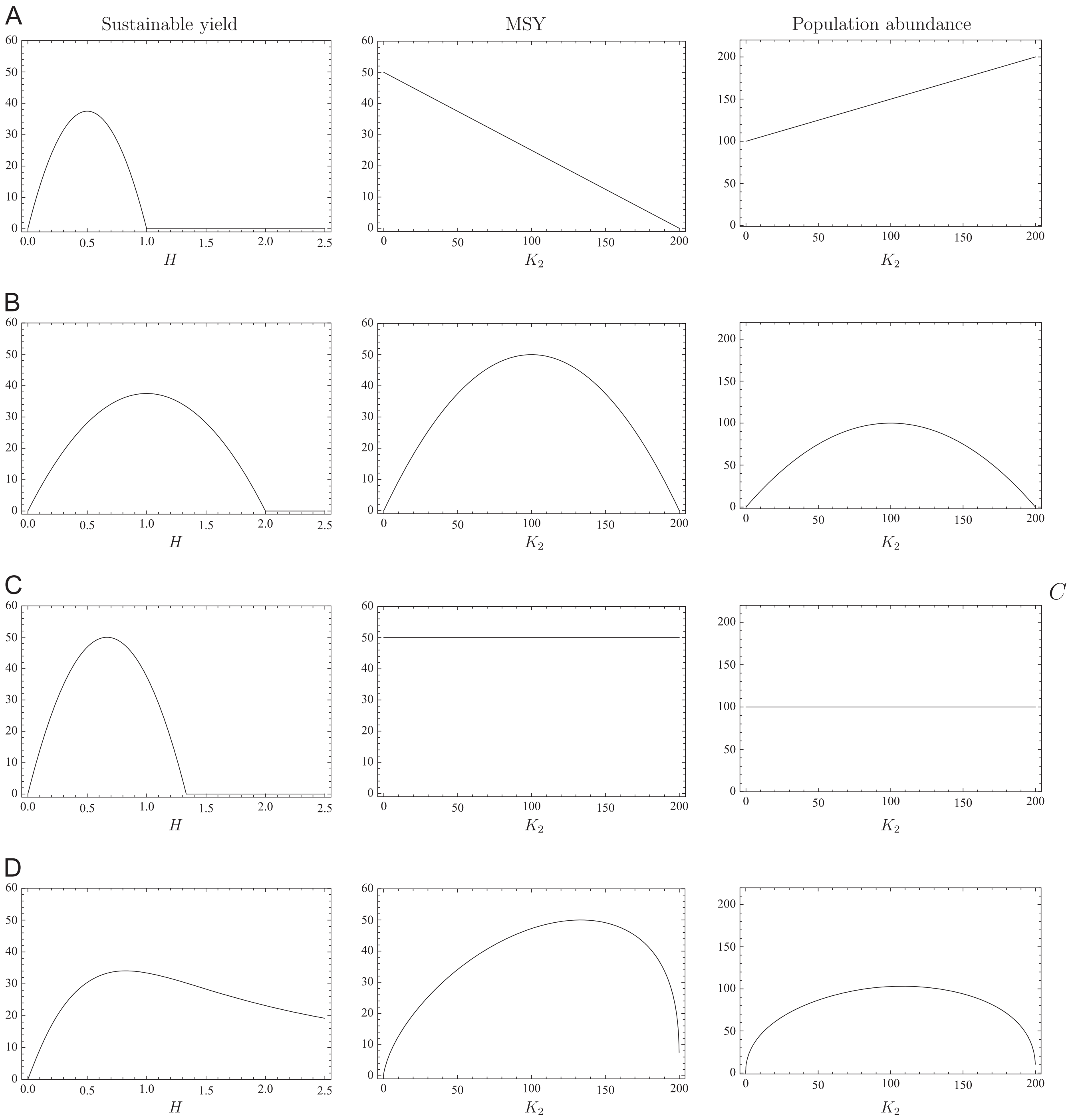

Fig. 1. Left panels show dependence of the sustainable yield (assuming environmental carrying capacities $K_1 = 150$ and $K_2 = 50$) on harvesting effort (H). Middle panels show the maximum sustainable yield (MSY), and the right panels show overall equilibrium population size at the optimal harvesting effort as a function of the environmental carrying capacity of the refuge (K_2) when total environmental carrying capacity is $K=200$. Panels A cover the following cases: (i) no dispersal between patches, (ii) fast density and harvest dependent distributional dynamics, and (iii) slow density and harvest dependent distributional dynamics. Panels B assume fast and density independent random dispersal (with corresponding distribution $u_1 = u_2 = 0.5$). Panels C cover the following cases: (i) balanced and density independent dispersal dynamics, (ii) fast density dependent distributional dynamics, and (iii) slow density dependent distributional dynamics. Panels D show results for density independent dispersal that operates on the same time scale as population dynamics (i.e., $\delta = 1$, $d_{12} = d_{21} = 1$ in model (1)). Other parameters used in simulations: $r=1$.