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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

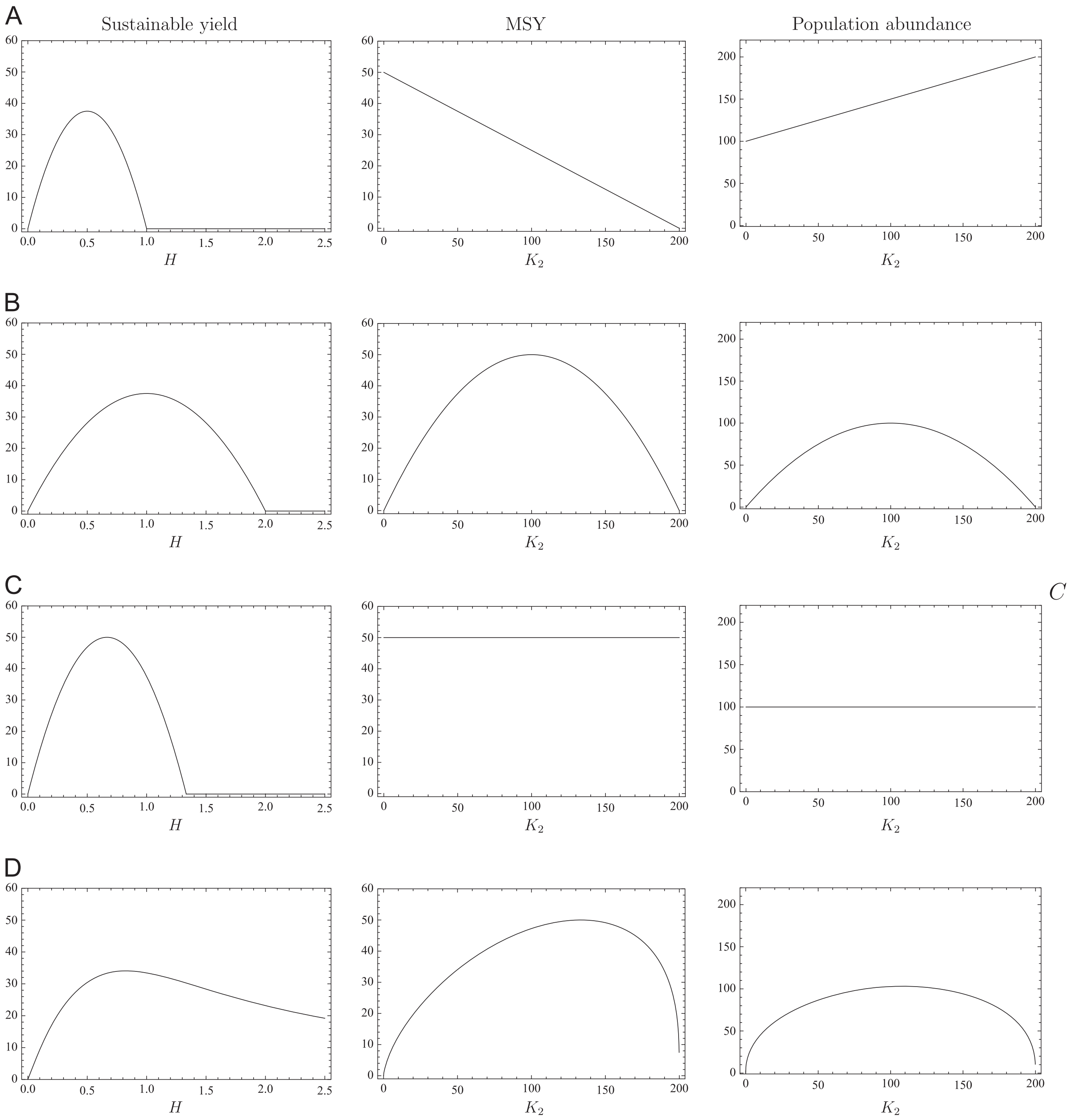

Fig. 1. Left panels show dependence of the sustainable yield (assuming environmental carrying capacities $K_1 = 150$ and $K_2 = 50$) on harvesting effort (H). Middle panels show the maximum sustainable yield (MSY), and the right panels show overall equilibrium population size at the optimal harvesting 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: $r=1$.

that dispersal can have very large effects on the impact of marine reserves. A general conclusion from these surveys of existing models and empirical knowledge is that refuges provide less benefit for highly movable species when compared to those that do not move, or move very little.

In this article we contrast density dependent vs. density independent dispersal modes. In particular, we focus on density dependent dispersal which assumes that animals move from the patch with a lower payoff to the patch with a higher payoff. We consider patch payoffs that are either density dependent and harvest independent, or density and harvest dependent. To analyze the resulting models we consider two different time scalings. Either population dynamics operate on a much (infinitely) slower time scale when compared with distributional dynamics or evolution of distributional dynamics is much slower when compared with population dynamics.

2. Models with density independent dispersal

We consider a single population in an environment consisting of two patches. The first, open patch, is the harvested area (of size A_1) while the second patch (of size A_2) is protected. The environmental carrying capacity κ of the whole area ($A = A_1 + A_2$), expressed as the number of fish per unit area, is assumed to be fixed. We assume that the population grows logistically with the uniform per capita population growth rate parameter r and patch specific environmental carrying capacity $K_i = \kappa A_i$, expressed as the number of fish per patch. Individuals are free to disperse between the two adjacent patches. Harvesting in the open patch 1 is described by the Gordon-Schaefer model (Schaefer, 1991; Clark, 1976 with the catchability coefficient q set to 1). Dispersal–population dynamics are (Kar and Matsuda, 2008)

$$\begin{aligned}\frac{dx_1}{dt} &= x_1 r\left(1-\frac{x_1}{K_1}\right) - Hx_1 - \delta(d_{12}x_1 - d_{21}x_2)\\ \frac{dx_2}{dt} &= x_2 r\left(1-\frac{x_2}{K_2}\right) - \delta(d_{21}x_2 - d_{12}x_1)\end{aligned} \tag{1}$$

where x_i is population abundance in patch i, H is the harvest effort, d_{ij} ($i,j=1,2$) is the probability of dispersing from patch i to patch j, and δ is the propensity of individuals to disperse. We start our analysis of model (1) with the simplest case where animals do not disperse (e.g., animals are sedentary).

2.1. Animals do not disperse

The case where animals do not disperse corresponds to setting $\delta=0$ in model (1). Population dynamics (1) then simplify to the classic Gordon-Schaefer harvesting model in the open patch with population growing logistically in the protected patch 2, i.e.,

$$\begin{aligned}\frac{dx_1}{dt} &= rx_1\left(1-\frac{x_1}{K_1}\right) - Hx_1,\\ \frac{dx_2}{dt} &= rx_2\left(1-\frac{x_2}{K_2}\right).\end{aligned} \tag{2}$$

Here x_1 and x_2 is the population abundance in the harvested patch and in the refuge, respectively. The classical result (Clark, 1976) shows that provided $r > H$, population dynamics converge to equilibrium

$$(x_1, x_2) = \left(\frac{K_1(r-H)}{r}, K_2\right) \tag{3}$$

with total population abundance

$$x = K - \frac{HK_1}{r}, \tag{4}$$

where $K = K_1 + K_2$. The sustainable yield in the open patch is

$$Y = Hx_1 = HK_1\left(1-\frac{H}{r}\right), \tag{5}$$

see Fig. 1A (left panel). This yield maximizes at harvest effort

$$H^* = \frac{r}{2}. \tag{6}$$

Substituting expression for H^* in (3) gives the population equilibrium under optimal harvesting $(x_1^*, x_2^*) = (\frac{K_1}{2}, K_2)$. Thus, the overall equilibrium population abundance is

$$x^* = \frac{K_1}{2} + K_2 = K - \frac{K_1}{2} \tag{7}$$

and the maximum sustainable yield (MSY) at this population equilibrium is

$$Y^* = \frac{rK_1}{4}. \tag{8}$$

Fig. 1A (middle panel) shows that as the protected area increases (i.e., K_2 increases) and the harvested area decreases, the MSY (8) linearly decreases and the overall equilibrium population size (7) linearly increases (Fig. 1A, right panel) up to the overall environmental carrying capacity K when all habitat is protected. These patterns clearly express the dilemma: Creating a protected area decreases the MSY (i.e., fishermen profit), but increases the overall population abundance. In the next sections we show that dispersal can change this antagonistic prediction.

2.2. Density independent and fast dispersal

If $u_1 = x_1/x$ and $u_2 = x_2/x$ is the population distribution between patches, from model (1) population dynamics for the total population abundance ($x = x_1 + x_2$) is

$$\frac{dx}{dt} = ru_1x\left(1-\frac{u_1x}{K_1}\right) - Hu_1x + ru_2x\left(1-\frac{u_2x}{K_2}\right). \tag{9}$$

When dispersal is fast (i.e., δ in model (1) is great) population distribution tracks instantaneously current population abundance. This means that at each population abundance, population distribution will be at an equilibrium that is obtained by solving equation

$$d_{12}x_1 - d_{21}x_2 = x(d_{12}u_1 - d_{21}u_2) = 0 \tag{10}$$

together with constraint $u_1 + u_2 = 1$. This yields density independent distribution

$$u_1 = \frac{d_{21}}{d_{12}+d_{21}}, \quad u_2 = \frac{d_{12}}{d_{12}+d_{21}}. \tag{11}$$

Model (9) with distribution (11) is much easier to analyze when compared to model (1). Provided harvest effort is not too high and satisfies

$$H < \frac{r}{u_1}, \tag{12}$$

negatively density dependent model (9) has a an asymptotically stable equilibrium

$$x = \frac{K_1K_2(r-Hu_1)}{r(K_2u_1^2 + K_1u_2^2)}. \tag{13}$$

The sustainable yield (Fig. 1B, left panel)

$$Y = Hu_1\frac{K_1K_2(r-Hu_1)}{r(K_2u_1^2 + K_1u_2^2)} \tag{14}$$

maximizes at harvesting effort

$$H^* = \frac{r}{2u_1}. \tag{15}$$

At this optimal harvesting effort population equilibrium is positive and equal to

$$x^* = \frac{K_1 K_2}{2(K_2 u_1^2 + K_1 u_2^2)} \tag{16}$$

(Fig. 1B, right panel) and the MSY at this equilibrium is

$$Y^* = H^* u_1 x^* = \frac{K_1 K_2 r}{4(K_1 u_2^2 + K_2 u_1^2)}, \tag{17}$$

Fig. 1B, middle panel. In contrast to the previous case of no dispersal, the MSY and the population equilibrium (13) are not monotone functions of the protected area size. Instead, there exists an optimal refuge size

$$K_2^* = K u_2 \tag{18}$$

at which both the MSY and the population abundance are maximized. We note that at the optimal protected area size K_2^* , $K_1^* = u_1 K$, the MSY equals to $rK/4$ and the equilibrium population abundance is $K/2$.

We remark that for higher harvesting efforts that do not satisfy inequality (12) the population is overexploited and goes extinct. This is because due to the open patch is depleted, i.e., $x_1 = 0$ and due to fast dispersal ($x_1 = u_1 x$) the overall population abundance must equal zero too.

2.3. Balanced dispersal

In contrast with the case of no dispersal, the equilibrium population abundance (13) for the fast dispersal between patches as a function of the refuge size (provided we assume that $K = K_1 + K_2$ is fixed) is generically a hump-shaped curve (qualitatively similar to Fig. 1B, right panel) that increases from 0 when $K_2 = 0$, reaches its maximum and decreases to 0 again when $K_2 = K$. In other words, when either the refuge or the open patch is small, the overall population abundance will be small too. This is the consequence of the mismatch between dispersal rates and environmental carrying capacities. For example, let us consider random dispersal (i.e., $d_{12} = d_{21} = 0.5$) and a refuge that is smaller relative to the open patch (i.e., K_2 is smaller than K_1). Thus, the refuge will be overpopulated due to influx of animals from the open patch which leads to a negative population growth rate in the refuge. In fact, for a fixed distribution, the patch that satisfies $K_i/K < u_i$ acts as a sink (Holt, 1997; Doncaster et al., 1997; Diffendorfer, 1998).

Kar and Matsuda (2008) assumed that dispersal was inversely proportional to patch carrying capacities, i.e.,

$$d_{12} = \frac{1}{K_1} \quad \text{and} \quad d_{21} = \frac{1}{K_2}. \tag{19}$$

Without harvesting, these dispersal rates correspond to balanced dispersal (McPeek and Holt, 1992; Holt and Barfield, 2001). Under balanced dispersal animal equilibrium population abundances in the two patches are the same as if there was no dispersal at all (i.e., $x_1^* = K_1$ and $x_2^* = K_2$ when $H = 0$). Thus, without harvesting and at the population equilibrium, both patches provide zero payoff (measured as the per capita population growth rate) and the population distribution corresponds to the IFD. When patches differ only in their area population distribution under balanced dispersal will match patch area distribution. Therefore, balanced dispersal is an important model that assumes patch occupancy is proportional to the patch area.

Under balanced dispersal population distribution matches distribution of environmental carrying capacities

$$u_i = \frac{K_i}{K}, \quad i = 1, 2. \tag{20}$$

Substituting this distribution in population equilibrium (13) gives the overall population abundance (4). Substituting (20) in (14) we obtain that the corresponding sustainable yield

$$Y = H K_1 \left(1 - \frac{H K_1}{rK}\right) \tag{21}$$

(Fig. 1C, left panel) maximizes at harvesting effort

$$H^* = \frac{Kr}{2K_1}. \tag{22}$$

The MSY is

$$Y^* = \frac{rK}{4} \tag{23}$$

(Fig. 1C, middle panel) and the corresponding population equilibrium is

$$x^* = \frac{K}{2}, \tag{24}$$

(Fig. 1C, right panel). We observe that under balanced dispersal, the MSY and the corresponding population abundance are independent of the refuge size. Thus, in the case of balanced dispersal when individuals do not react to increased harvest risk in the open patch, there is no dilemma. In fact, creation of protected area does not influence neither the MSY nor the population abundance.

The prediction that the MSY does not depend on the open patch environmental carrying capacity is somewhat counterintuitive, because even if the open patch is very small, the MSY should be the same as if there was no protected area. The reason is that as the open patch decreases, the optimal harvest effort (22) should increase. Thus, when the open patch is too small, the harvest effort is unrealistically high. In reality, the MSY starts to decrease once the high harvest rates (22) cannot be met.

2.4. Density independent dispersal when distributional and population dynamics operate on similar time scales

Now we want to compare our predictions for fast animal dispersal with predictions obtained from model (1) without assuming fast dispersal. Takeuchi (1996) proved that when an interior equilibrium of model (1) exists, it is globally asymptotically stable for any density independent dispersal rates. Although computer algebra software such as Mathematica do calculate the interior equilibrium for model (1), the resulting formula is too complex for further analysis. Fig. 1D shows numerical results when population and dispersal dynamics operate on the same time scale (i.e., $\delta = 1$ in model (1)). This is an intermediate case between no dispersal ($\delta = 0$, Fig. 1A) and infinitely fast density independent dispersal ($\delta \to \infty$, Fig. 1B). Numerical simulations show that the dilemma caused by creating a protected area diminishes as dispersal speed increases. Indeed, the mismatch between the MSY and the maximum population abundance is maximal when there is no dispersal (Fig. 1A). In this case the MSY maximizes when no protected area exists, while the population abundance maximizes when the whole habitat is protected (i.e., when harvesting ceases). When dispersal is infinitely fast, no dilemma exists because the MSY and the population size are maximized at the same protected area size (Fig. 1B for unbalanced dispersal). This shows that as dispersal speed increases, the dilemma gets weaker. For example, Fig. 1D shows that for $\delta = 1$ the MSY maximizes at approx. $K_2 = 133.3$ while the equilibrium population size maximizes at approx. $K_2 = 108.5$.

Fig. 2 compares unbalanced dispersal (left panels) with balanced dispersal (right panels) as a function of dispersal speed (δ). Using Mathematica we calculated symbolically equilibrium population abundance. The resulting formulas are very complex. Then we numerically calculated the harvest effort that maximizes the yield in the open patch. Using this optimal harvest effort we calculated the maximum sustainable yield and the population

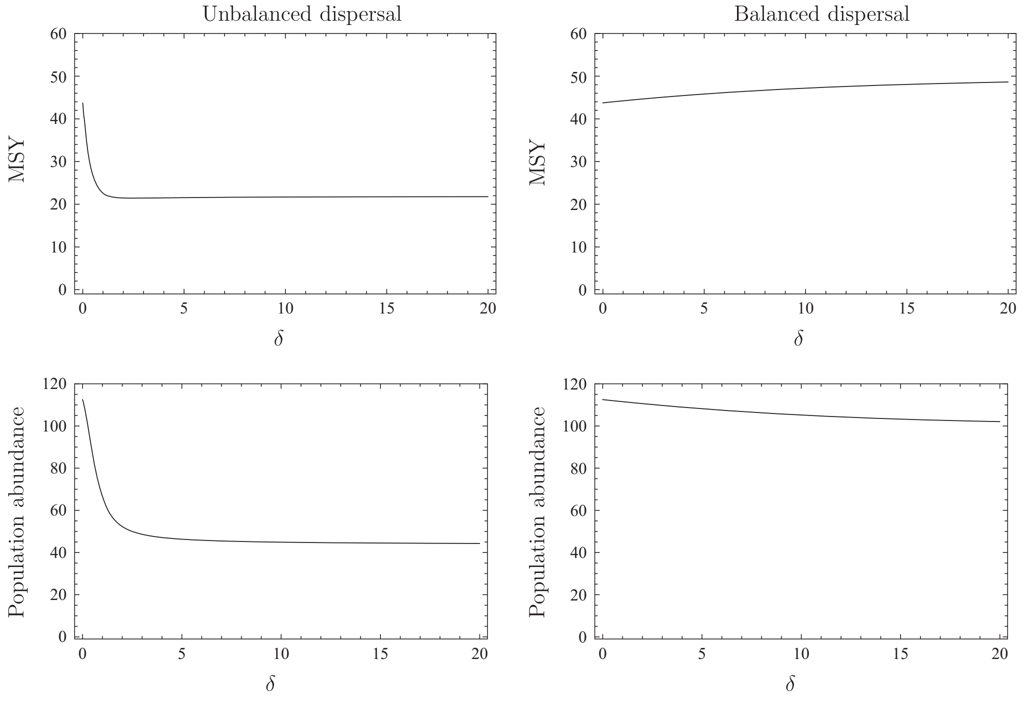

Fig. 2. Left panels show dependence of the overall equilibrium population abundance and the maximum sustainable yield (MSY) on dispersal speed δ in model (1) for unbalanced dispersal with equal patch preferences ($d_{12} = d_{21} = 1$) and the refuge size set to $K_2 = 25$. Right panels assume balanced dispersal rates $d_{12} = r/K_1$ and $d_{21} = 1/K_2$. Other parameters used in simulations: $r = 1$, $K_1 = 175$.

equilibrium. For no dispersal ($\delta = 0$) the MSY and the population abundance in Fig. 2 are those shown in Fig. 1, panels A when $K_2 = 25$. For large dispersal rates the values in Fig. 2, left panels for unbalanced dispersal (right panels for balanced dispersal) converge to those shown in Fig. 1, panels B (panels C).

3. Models with density dependent dispersal

So far we have considered density independent dispersal by assuming that dispersal rates between the open patch and the protected patch are independent of population abundance. Now we consider density dependent dispersal with dispersal rates depending on population numbers (e.g., Takashina and Mougi, 2014). We also assume that animals adjust their dispersal on patch occupancy and/or harvest risk in the open patch and they do it in the way that increases their fitness. Animal fitness is calculated as the average patch payoff measured by the per capita population growth rate. We consider two cases of density dependent dispersal: (i) fast distributional dynamics that track current population densities, or (ii) slow distributional dynamics that tracks current population distribution. These two cases describe two ends of spectra: Either distributional dynamics run on an infinitely faster time scale than population dynamics, or population dynamics run on an infinitely faster time scale than distributional dynamics. We will ask whether these two opposite time scalings lead to the same qualitative predictions. It is likely that if they do, the intermediate cases where time scales are not such strictly separated will be qualitatively similar. Finally we also consider population-dispersal dynamics (1) when dispersal speed is intermediate.

3.1. Fast density dependent and harvest independent distributional dynamics

In this section we consider density dependent dispersal with individuals dispersing preferentially to the patch with the higher payoff. The payoff in the harvested patch is $V_1 = r(1-\frac{u_1 x}{K_1})$ while the payoff in the refuge is $V_2 = r(1-\frac{u_2 x}{K_2})$. In other words we assume that animals adjust their dispersal to patch quality but they disregard harvest mortality in the open patch. Fitness of an individual that spends proportion v_i of its lifetime in patch i when population distribution is (u_1, u_2) is defined as the average payoff

$$W(v_1, u_1) = r v_1 \left(1 - \frac{u_1 x}{K_1}\right) + r v_2 \left(1 - \frac{u_2 x}{K_2}\right). \tag{25}$$

The evolutionarily stable distribution for this fitness function is called the ideal free distribution (IFD; Fretwell and Lucas, 1969; Křivan et al., 2008). At the IFD patch payoffs must be the same $V_1 = V_2$ which yields (Křivan et al., 2008)

$$u_1 = \frac{K_1}{K}. \tag{26}$$

The IFD for fitness function (25) is independent of the population abundance, and both patches are always occupied. Substituting (26) in model (9) leads to population dynamics

$$\frac{dx}{dt} = x \frac{r(K-x) - HK_1}{K}. \tag{27}$$

For low harvest rates satisfying $H < rK/K_1$ population abundance converges to equilibrium (4), with the corresponding sustainable yield (21), the MSY (23), and the corresponding equilibrium population abundance (24) that are identical to balanced and density independent dispersal (Fig. 1C). Thus, both population equilibrium x^* as well as the MSY are independent of the harvest effort exactly as in the case of balanced and density independent dispersal.

3.2. Fast density and harvest dependent distributional dynamics

Now we assume that the payoff in the open patch is harvest independent, i.e.,

$$V_1 = r\left(1 - \frac{u_1 x}{K_1}\right) - H \tag{28}$$

and in the protected patch $V_2=r(1-\frac{u_2x}{K_2})$. Fitness of an individual with strategy (v_1,v_2) when population distribution is (u_1,u_2) is then

$$W(v_1,u_1)=rv_1\left(1-\frac{u_1x}{K_1}\right)-Hv_1+rv_2\left(1-\frac{u_2x}{K_2}\right). \tag{29}$$

This fitness assumes that individuals react to harvest mortality in the open patch 1. Solving the equation $V_1=V_2$ we obtain the IFD

$$u_1=\begin{cases}\frac{K_1(rx-HK_2)}{rKx} & \text{if } x\ge\frac{K_2H}{r}\\ 0 & \text{if } x<\frac{K_2H}{r}.\end{cases} \tag{30}$$

Thus, when at low population densities, individuals occupy preferentially the refuge because there is no mortality due to harvesting and density dependence is low there. However, when the overall population abundance meets the threshold K_2H/r, the payoff in unpopulated open patch equalizes with the payoff in the refuge, and, as the population abundance further increases, both patches get occupied.

Population dynamics (9) at the IFD (30) are

$$\frac{dx}{dt}=\begin{cases}\frac{x(r(K-x)-HK_1)}{K} & \text{if } x\ge\frac{K_2H}{r}\\ rx\left(1-\frac{x}{K_2}\right) & \text{if } x<\frac{K_2H}{r}.\end{cases} \tag{31}$$

To analyze equilibria of model (31) we consider two cases. When harvest rate in the open patch is low $(H<r)$ both patches are occupied at the population equilibrium

$$x=K-\frac{HK_1}{r} \tag{32}$$

and the population distribution among patches is

$$u_1=\frac{K_1(r-H)}{Kr-HK_1}. \tag{33}$$

The sustainable yield at this population equilibrium (5), the MSY (8) and the corresponding population equilibrium (7) are identical to the case of no dispersal between patches (Fig. 1A). Here we again observe the dilemma: increasing the refuge size decreases the MSY, but increases population abundance.

When harvest rate in the open patch is high $(H>r)$ all individuals occupy protected patch 2 where equilibrium population abundance is K_2 and the harvest rate drops to 0. We observe that in contrast to the case of density independent dispersal, population survives in the protected patch despite that there are no individuals in the open patch.

3.3. Slow density dependent and harvest independent distributional dynamics

In contrast to the previous two sections, we assume now that animals adjust their patch preferences in the direction of a higher fitness very slowly when compared to population dynamics. In fact, we consider evolution of dispersal rates by assuming that equilibrium population abundance tracks current population distribution. We start our analysis by assuming that harvest rate is not too high and satisfies $H<r/u_1$ at current population distribution (u_1,u_2). Then model (9) has a globally stable population equilibrium (13). Fitness of an individual that spends proportion v_i of its lifetime in patch i when population distribution is (u_1,u_2), is given by (25). This fitness assumes that animals do not react to harvest mortality. The evolution of distribution is then described by the canonical equation of adaptive dynamics (e.g., Dercole and Rinaldi, 2008; Metz, 2012)

$$\frac{du_1}{dt}=k(u_1)\left.\frac{\partial W(v_1,u_1)}{\partial v_1}\right|_{v_1=u_1}=k(u_1)\frac{(r-Hu_1)(K_1-Ku_1)}{K_1u_2^2+K_2u_1^2} \tag{34}$$

where k is a non-negative function measuring the speed of adaptation (we assume that $k(0)=k(1)=0$) and the partial derivative is evaluated at the population equilibrium (13). Distributions r/H and K_1/K are (non-trivial) equilibria of model (34). First, we assume that $H<rK/K_1$. Then equilibrium distribution $u_1=K_1/K<r/H$ is asymptotically stable because at this equilibrium distributional dynamics (34) are negatively frequency dependent. At this distribution, population equilibrium is $x=K-\frac{HK_1}{r}$. The sustainable yield at this equilibrium (21), the MSY (23) and the corresponding population abundance (24) are identical to the case of balanced and density independent fast dispersal (Fig. 1C).

Second, if the harvest rate is high, i.e., $rK/K_1<H$, then the other equilibrium $u_1=r/H$ of (34) is locally stable. However, at this distributional equilibrium population is globally depleted.

3.4. Slow density and harvest dependent distributional dynamics

Now we assume that animals react not only to patch quality but also to harvest risk, i.e., fitness of an individual that spends proportion v_i of its lifetime in patch i when population distribution is (u_1,u_2) is given by (29). The corresponding canonical equation of adaptive dynamics is

$$\frac{du_1}{dt}=\frac{K_1(r-H)+(HK_1-Kr)u_1}{K_1u_2^2+K_2u_1^2}. \tag{35}$$

Assuming that $H<r$, the distributional equilibrium of the canonical equation (35)

$$u_1=\frac{K_1(r-H)}{Kr-HK_1} \tag{36}$$

is positive and asymptotically stable (since $H<r$ implies $H<rK/K_1$ as $K_1<K$). The population equilibrium at this distribution is

$$x=K-\frac{HK_1}{r}. \tag{37}$$

The sustainable yield at this equilibrium (4), the MSY (8) and the corresponding population abundance (24) are identical to the case of fast density and harvest dependent distributional dynamics (Fig. 1A). Again, the dilemma arises in this case.

3.5. Distributional and population dynamics operate on similar time-scales

If distributional and population dynamics operate on similar time scales, we need to specify dependence of dispersal rates on population abundance in model (1). A strategic model that assumes density and harvest dependent dispersal in the direction of increasing fitness can be described by the following population–dispersal dynamics (Cressman and Křivan, 2013)

$$\begin{aligned}\frac{dx_1}{dt}&=x_1f_1(x_1)-Hx_1+\delta\frac{x_1x_2}{x_1+x_2}(f_1(x_1)-H-f_2(x_2)),\\ \frac{dx_2}{dt}&=x_2f_2(x_2)+\delta\frac{x_1x_2}{x_1+x_2}(f_2(x_2)-f_1(x_1)+H).\end{aligned} \tag{38}$$

The interior population equilibrium of this model is the same as for model (2) with no dispersal and Appendix A shows that it is locally asymptotically stable independently of dispersal speed whenever population growth in both patches is negatively density dependent (i.e., $f_i'<0$). In particular, this holds when $f_i(x_i)=r(1-x_i/K_i)$ as we have assumed in this article.

4. Discussion

In this article we study effects of dispersal modes between a harvested patch and an unharvested protected area (refuge) on the maximum sustainable yield and equilibrium population abundance.

Creation of protected areas (e.g., marine protected area) is believed to lead to a dilemma (Gordon, 1954): it decreases the maximum sustainable yield while it increases population abundance. The Gordon–Schaefer harvesting model without any dispersal makes such a prediction (Fig. 1A). In this article we show that dispersal can change these trends. In particular, the dilemma does not arise when dispersal between patches is fast and density independent (Fig. 1B), or dispersal is either fast or slow and in the direction of a higher fitness when animals disregard harvest mortality risk (Fig. 1C). When animals adaptively react to harvesting mortality in the open patch, the maximum sustainable yield and the corresponding population abundance are the same as in the case of no dispersal (Fig. 1A).

To analyze the effects of dispersal modes on effectiveness of protected areas we assume time scale separation between distributional and population dynamics. Such scaling is useful as it allows for mathematical analysis of models that are otherwise difficult or impossible to analyze. In particular, if dispersal operates on the fast time scale, the two population-dispersal equations are reduced to a single differential equation that describes the overall population dynamics. In the case when distributional dynamics are slow, the resulting model for population distribution is described by the canonical equation of adaptive dynamics (e.g., Dercole and Rinaldi, 2008; Metz, 2012). In both cases the resulting equations are easy to analyze.

In the case of density independent and (infinitely) fast dispersal between the open patch and the protected patch we show that the maximum sustainable yield and the corresponding population abundance are unimodal curves of the refuge size (Fig. 1B, Table 1). Both these curves are maximized at the same refuge size, so if a protected area of that size can be established, there will be no trade-off between maximizing sustainable yield and the equilibrium population abundance. In general, the optimum refuge size depends on animal patch preferences.

When dispersal is balanced (McPeek and Holt, 1992; Holt and Barfield, 2001; Cressman and Křivan, 2013), i.e., population distribution matches patch environmental carrying capacities, the MSY and the overall population abundance are independent of the refuge size (Fig. 1C, Table 1). This counterintuitive prediction depends on the fact that the optimal harvest effort is inversely proportional to the open patch environmental carrying capacity. Thus, when the open patch becomes too small, the optimal harvest effort cannot be met and the MSY will eventually decrease.

We also consider density dependent dispersal rates. In this case we assume that distributional dynamics are either very fast so that at each population abundance, the population distribution is at an equilibrium, or very slow so that at each population distribution, the population abundance is at an equilibrium. Both of these approaches assume that the net dispersal is in the direction of increasing fitness. We define animal fitness as the average patch payoff and we assume two possibilities: Either dispersal is only density dependent, or it is both density and harvest dependent. In the former case animals disregard mortality risk associated with harvesting, while in the second case harvesting mortality risk is a part of fitness. Both these approaches assume negative density dependent patch payoffs. It is interesting to note that whether distributional dynamics are fast or slow does not influence the optimal harvest rate, the MSY and the corresponding population equilibrium (Table 1). This suggests that even when time scales are not so strictly separated, the results will be qualitatively similar. What does matter is the choice of the fitness function. If the fitness function disregards harvest mortality in the open patch, results are the same as in the case of the fast balanced density independent dispersal (Fig. 1C, Table 1). In this case no dilemma associated with creation of a protected area arises. When harvest mortality in the open patch is included in the fitness, predictions are identical to those of the classical Gordon–Schaefer harvesting model (Fig. 1A, Table 1). In this case there is a strong trade-off between the MSY and the population abundance.

We also study the general case where no time-scale separation between distributional and population processes is assumed. In the case of density independent dispersal the expression for population equilibrium is too complicated for mathematical analysis and we used numerical simulations (such as those shown in Fig. 1D for the case $\delta = 1$). These dependencies are intermediate cases between no dispersal (Fig. 1A) and infinitely fast dispersal (Fig. 1B). As dispersal speed increases, the dilemma gets weaker when compared to the case of no dispersal because the MSY and the population equilibrium will be maximized at intermediate protected area sizes. This we see in Fig. 1D where the MSY maximizes at $K_2 = 133$ and the population abundance at $K_2 = 108$. As dispersal rates converge to infinity, these two points of maxima converge to the same value. Dependence of equilibrium population abundance and the MSY on the dispersal speed is shown in Fig. 2. Left panels show results for unbalanced dispersal, while the right panels assume balanced dispersal between patches.

A general predictions from our models is that all types of dispersal considered in this article diminish the positive effect of the protected area on population abundance when compared with the case of no dispersal (cf. right panels in Fig. 1A vs. B–D). This result corresponds to similar predictions that marine protected areas will provide fewer benefits to populations that disperse more (Gerber et al., 2003; Grüss et al., 2011). On the other hand, the MSY can be either larger or smaller when animals disperse depending on the refuge size (cf. middle panels in Fig. 1A vs. B–D). However, to achieve a larger MSY under animal dispersal, the protected area must be large enough, which may be difficult to achieve in reality.

Table 1
Overview of model results.

Dispersal	MSY Y^*	Equilibrium Population Size x^*	Panel in Fig. 1
No dispersal (Section 2.1) Fast density and harvest dependent dispersal (Section 3.2) Slow density and harvest dependent dispersal (Section 3.4)	$\frac{rK_1}{4}$	$K - \frac{K_1}{2}$	A
Density independent and fast dispersal (Section 2.2)	$\frac{K_1 K_2 r}{4(K_1 u_2^2 + K_2 u_1^2)}$	$\frac{K_1 K_2}{2(K_2 u_1^2 + K_1 u_2^2)}$	B
Balanced density independent dispersal (Section 2.3) Fast density dependent and harvest independent dispersal (Section 3.1) Slow density dependent and harvest independent dispersal (Section 3.3)	$\frac{rK}{4}$	$\frac{K}{2}$	C

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Appendix A. Stability of the interior equilibrium for model (38)

The Jacobian matrix evaluated at the interior equilibrium ($f_1(x_1) = H_1$ and $f_2(x_2) = 0$) is

$$J = \begin{pmatrix} (x_1 + \delta\frac{x_1x_2}{x_1+x_2}) f_1{}'(x_1) & -\delta\frac{x_1x_2}{x_1+x_2} f_2{}'(x_2) \\ -\delta\frac{x_1x_2}{x_1+x_2} f_1{}'(x_1) - 2\delta\frac{x_2^2}{(x_1+x_2)^2} H & (x_2 + \delta\frac{x_1x_2}{x_1+x_2}) f_2{}'(x_2) - 2\,H\delta\frac{x_1^2}{(x_1+x_2)^2} \end{pmatrix}.$$

As we assume $f_i{}' < 0$, the trace of matrix

$$\mathrm{tr}J = \frac{-2x_1^2\delta H + (x_1+x_2)(x_1(x_1+x_2+x_2\delta) f_1{}'(x_1) + x_2(x_1+x_2+x_1\delta) f_2{}'(x_2))}{(x_1+x_2)^2}$$

is negative and the determinant of J

$$\det J = \frac{x_1(x_2(x_1+x_2)^3(1+\delta) f_1{}'(x_1) f_2{}'(x_2) - 2\delta H(x_1^2(x_1+x_2+x_2\delta) f_1{}'(x_1) + x_2^3\delta f_2{}'(x_2)))}{(x_1+x_2)^3}$$

is positive. Thus, the interior equilibrium, provided it exists, is locally asymptotically stable independently of dispersal speed.

References

Berec, M., Křivan, V., Berec, L., 2006. Asymmetric competition, body size and foraging tactics: testing an ideal free distribution in two competing fish species. Evolutionary Ecology Research 8, 929–942.

Beverton, R.J.H., 1953. Some observations on the principles of fishery regulation. J. Cons. int. Explor. Mer, 56–68.

Brown, J.S., Kotler, B.P., 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7, 999–1014.

Cantrell, R.S., Cosner, C., Lou, Y., 2010. Evolution of dispersal and the ideal free distribution. Mathematical Biosciences and Engineering 7, 17–36.

Cantrell, R.S., Cosner, C., Lou, Y., 2012. Evolutionary stability of ideal free dispersal strategies in patchy environments. Journal of Mathematical Biology 65, 943–965.

Clark, C.W., 1976. Mathematical Bioeconomics: The Optimal Management Of Renewable Resources. John Wiley & Sons, New York, NY, USA.

Cressman, R., Křivan, V., 2006. Migration dynamics for the ideal free distribution. American Naturalist 168, 384–397.

Cressman, R., Křivan, V., 2013. Two-patch population models with adaptive dispersal: the effects of varying dispersal speeds. J. Math. Biol. 67, 329–358.

Dercole, F., Rinaldi, S., 2008. Analysis of evolutionary processes. The adaptive dynamics approach and its applications. Princeton University Press, Princeton.

Diffendorfer, J.E., 1998. Testing models of source-sink dynamics and balanced dispersal. Oikos 81, 417–433.

Doncaster, C.P., Clobert, J., Doligez, B., Gustafsson, L., Danchin, E., 1997. Balanced dispersal between spatially varying local populations: an alternative to the source-sink model. American Naturalist 150, 425–445.

Fretwell, D.S., Lucas, H.L., 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19, 16–32.

Gerber, L.R., Botsford, L.W., Hastings, A., Possingham, H.P., Gaines, S.D., Palumbi, S.R., Andelman, S., 2003. Population models for marine reserve design: a retrospective and prospective synthesis. Ecological Applications 13, S47–S64.

Gordon, H.S., 1954. The economic theory of a common-property resource: the fishery. Journal of Political Economy 62, 124–142.

Grüss, A., Kaplan, D.M., Guénette, S., Roberts, C.M., Botsford, L.W., 2011. Consequences of adult and juvenile movement for marine protected areas. Biological Conservation 144, 692–702.

Hastings, A., 1983. Can spatial variation alone lead to selection for dispersal? Theoretical Population Biology 24, 244–251.

Haugen, T.O., Winfield, I.J., Vollestad, L.A., Fletcher, J.M., James, J.B., Stenseth, N.C., 2006. The ideal free pike: 50 years of fitness-maximizing dispersal in windermere. Proceedings of the Royal Society B: Biological Sciences 273, 2917–2924.

Holt, R.D., 1997. On the evolutionary stability of sink populations. Evolutionary Ecology 11, 723–731.

Holt, R.D., Barfield, M., 2001. On the relationship between the ideal-free distribution and the evolution of dispersal. In: Danchin, J.C.E., Dhondt, A., Nichols, J. (Eds.), Dispersal. Oxford University Press, pp. 83–95.

Ives, A.R., Dobson, A.P., 1987. Antipredator behaviour and the population dynamics of simple predator-prey systems. American Naturalist 130, 431–447.

Kar, T.K., Matsuda, H., 2008. A bioeconomic model of a single-species fishery with a marine reserve. Journal of Environmental Management 86, 171–180.

Kennedy, M., Gray, R.D., 1993. Can ecological theory predict the distribution of foraging animals? a critical analysis of experiments on the ideal free distribution. Oikos 68, 158–166.

Křivan, V., 1998. Effects of optimal antipredator behavior of prey on predator-prey dynamics: role of refuges. Theoretical Population Biology 53, 131–142.

Křivan, V., 2013. Behavioral refuges and predator-prey coexistence. Journal of Theoretical Biology 339, 112–121.

Křivan, V., Cressman, R., Schneider, C., 2008. The ideal free distribution: a review and synthesis of the game theoretic perspective. Theoretical Population Biology 73, 403–425.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68, 619–640.

McPeek, M.A., Holt, R.D., 1992. The evolution of dispersal in spatially and temporally varying environments. American Naturalist 140, 1010–1027.

Metz, J.A.J., 2012. Adaptive dynamics. In: Hastings, A., Gross, L.J. (Eds.), Encyclopedia Of Theoretical Ecology. University of California Press, Berkeley and Los Angeles, California, pp. 7–17.

Milinski, M., 1979. An evolutionarily stable feeding strategy in sticklebacks. Zeitschrift für Tierpsychologie 51, 36–40.

Neubert, M.G., Herrera, G.E., 2008. Triple benefits from spatial resource management. Theoretical Ecology 1, 5–12.

Peacor, S.D., Werner, E.E., 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. Proceedings of the National Academy of Sciences of the USA 98, 3904–3908.

Ruxton, G.D., 1995. Short term refuge use and stability of predator-prey models. Theoretical Population Biology 47, 1–17.

Schaefer, M., 1991. Some aspects of the dynamics of population important to the management of the commercial marine fisheries. Bulletin of Mathematical Biology 53, 253–279.

Sih, A., 1980. Optimal behavior: Can foragers balance two conflicting demands?. Science 210, 1041–1043.

Sih, A., 1986. Antipredator responses and the perception of danger by mosquito larvae. Ecology 67, 434–441.

Sih, A., 1987. Prey refuges and predator-prey stability. Theoretical Population Biology 31, 1–12.

Takashina, N., Mougi, A., 2014. Effects of marine protected areas on overfished fishing stocks with multiple stable states. Journal of Theoretical Biology 341, 64–70.

Takeuchi, Y., 1996. Global dynamical properties of Lotka-Volterra systems. World Scientific Publishing Company, Singapore.