Model of two competing populations in two habitats with migration: application to optimal marine protected area size.

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Highlights

1. We consider a system of two competing populations with asymmetric migrations between two habitats.
2. We obtain equilibrium population sizes for zero, sufficiently small and infinite migration rates.
3. The coexistence condition for two competing species in a perfectly mixed habitat is derived.
4. Harvest mortality is added to the system and the maximum sustainable yield (MSY) is calculated.
5. The conditions under which a no-harvesting zone (e.g., marine protected area) can increase MSY are evaluated.

Abstract

The standard model of a single population fragmented into two patches connected by migration, was first introduced in the 1970s by Freedman and Waltman, since generating long-term research interest, though its full analysis for arbitrary values of migration rate has only been completed relatively recently. Here, we present a model of two competing species in a two-patch habitat with migrations between patches. We derive equilibrium solutions of this model for three cases of migration rate resulting in isolated, well-mixed and semi-isolated habitats. We evaluate the full range of effects of habitat, life-history and migration parameters on population sizes. Finally, we add harvesting mortality and define conditions under which introduction of a no-harvesting (protected area) may lead to increased maximum sustainable yield. The results have applications in mixed fishery management and the design of wildlife protection zones, including marine protected areas (MPAs).

Keywords: Multi-patch population dynamics, Migration, Species coexistence, Ideal free distribution, Multi-species MSY, MPA

1. Introduction

The issue of dispersal and migration has been one of core concern in ecology and conservation since the 1970s (SLOSS debate, Hanski, 1999), after the first basic 1x2-migration model (one species migrating between two patches) was considered by Freedman and Waltman (1977). Over the decades, much effort has been focused on the development and analysis of more general space-continuous reaction-diffusion and competition-diffusion models (Lou 2006) as well as the evolutionary consequences of migration (Hutson et al. 2003). Continuous models have produced several remarkable results, but their application to ecology has been limited due to the assumption of strict functional relationship between growth rate and carrying capacity (De Angelis et al., 2016). This assumption reduces the influence of the environment on the population to a function of a single variable, permitting the derivation of compact solutions; but it reduces the generality of continuous models. This problem with general biological interpretation of the results has revived interest in 1x2 (one species migrating between two patches) models, which do not constrain the relationship between growth rate and carrying capacity and allow direct experimental verification (Zhang et al. 2017). More recently, a complete analysis of the 1x2 model for any value of the migration rate in cases of symmetric (Arditi et al. 2015) and asymmetric (Arditi et al. 2018, Wu et al. 2020) migration has been completed. Most recently, Takashina (2020) developed a two-patch, single population model (based on Logistic-Shaefer dynamics) to enable the optimal size of marine protected areas (MPAs) to be calculated, taking account of adult (density-dependent) dispersal. The two patches (representing a fishing ground and marine reserve) set up a source-sink dynamic with migration, which was analysed only for cases where migration rate is much greater than population growth rate.

Here, we consider two competing species in two patches (2x2). We analyse the model at three (zero, sufficiently small and infinity) ranges of migration rates to investigate the effect of migration rates on equilibrium population sizes and species coexistence conditions. Then, we add harvesting pressure to the previous model and analyse how two-species maximum sustainable yield (MSY) is affected by interspecific competition and species migrations. Finally, we formulate the protected area optimal choice problem, i.e., how to divide the total area into protected and exploited parts, so that MSY does not decrease or, under certain conditions, may even increase. Using a simple example, we illustrate a possible solution to this problem.

This is of practical importance because management of mobile wildlife populations often involves nature reserves or MPAs adjacent to or surrounded by areas in which hunting, or harvesting are permitted at a higher level. The effectiveness of a protected area depends on its spatial extent relative to the dispersion rate of the organisms for which it is intended (Botsford et al., 2001; Moffitt et al., 2011; Gruss et al. 2011; Green et al. 2015). Conflict between harvesting and conservation goals can be mitigated by the ‘spill-over effect’ whereby the natural dispersion of harvestable organisms from the protected area compensates for area lost to harvesting, especially in fisheries (e.g., DiLorenzo et al. 2016), but also might exasperate wildlife / domestic stock conflict (e.g., Holmern et al. 2007). Population models which include migration or dispersal are needed to determine the optimal (or minimum viable) size of reserves, such as MPAs (reviewed in Botsford et al. 2019), but most work so far has concentrated on larval dispersal in marine cases and on single populations without reference to trophic or competitive interactions.

Description of the model

Assume that two competing species m and n follow the standard Lotka-Volterra competition model:

$$\begin{cases} \dfrac{dm}{dt} = rm\left(1 - \dfrac{m}{K} - \dfrac{\alpha n}{K}\right) \\ \dfrac{dn}{dt} = sn\left(1 - \dfrac{n}{L} - \dfrac{\beta m}{L}\right) \end{cases}, \tag{0}$$

where K, L are carrying capacities, β and α are competition interaction coefficients, r and s are net growth rates for species m and n respectively. This model assumes that populations are perfectly mixed in space and may coexist in a common homogeneous habitat. To introduce habitat fragmentation, it commonly accepted to assume (Arditi et al. 2015) that subpopulations on each patch follow a local competition model and patches are linked by migrations (**Fig.1**). In the simple case of two patches and asymmetric migrations between sites, the model (0) can be rewritten as:

$$\begin{cases} \dfrac{dm_1}{dt} = r_1 m_1\left(1 - \dfrac{m_1}{K_1} - \dfrac{\alpha_1 n_1}{K_1}\right) + \varepsilon D_m (m_2 - S_m m_1) \\ \dfrac{dm_2}{dt} = r_2 m_2\left(1 - \dfrac{m_2}{K_2} - \dfrac{\alpha_2 n_2}{K_2}\right) + \varepsilon D_m (S_m m_1 - m_2) \\ \dfrac{dn_1}{dt} = s_1 n_1\left(1 - \dfrac{n_1}{L_1} - \dfrac{\beta_1 m_1}{L_1}\right) + \varepsilon D_n (n_2 - S_n n_1) \\ \dfrac{dn_2}{dt} = s_2 n_2\left(1 - \dfrac{n_2}{L_2} - \dfrac{\beta_2 m_2}{L_2}\right) + \varepsilon D_n (S_n n_1 - n_2) \end{cases}, \tag{1}$$

where K_i, L_i are carrying capacities, α_i β_i competition interaction coefficients and r_i, s_i net growth rates in habitat i for species m and n, respectively. Also, D_m, S_m and D_n, S_n are specific migration rates and asymmetry coefficients for species m and n. Finally, ε is scale parameter, which defines magnitude or intensity of migrations. Thus, the resulting migration flow rates can be calculated as $\varepsilon D_k S_k$. All parameters are assumed to be positive; hereafter, without loss of generality, we assume that $D_m > D_n$ or m is “fast-migrating” and n is “slow-migrating” species. The asymmetry coefficients represent a consistent bias in transition rate among habitats, which would normally arise from directed searching by the organisms to result in what Cressman and Křivan, 2013 termed ‘adaptive dispersion’. S could be expanded to represent, e.g., a response to resource gradient. Particularly, the asymmetry coefficient $S = 0$ means that the first habitat is a “pseudo-sink” (Watkinson and Sutherland 1995) i.e. only inward migration is present; $S = 1$ means that species have no preferences to any habitat and $S > 1$ means that the first habitat is a “pseudo-source” i.e. species prefer migrating to the second habitat. It should be noted that the terms "pseudo-source" and "pseudo-sink" differ from similar terms "source" and "sink" in that in the first case only migration flows are considered, while in the second case the difference in net growth rates is also considered. e.g., “sink” means that the net growth rate is negative for a given habitat, whereas "pseudo-sink" means that there is an inflow into the given area.

2. Model of two competing species migrating between two patches at different migration magnitudes

In this section, we consider equilibrium solutions of the system (1). In general, this system does not have a convenient compact form of solutions for a full set of parameters and especially for arbitrary magnitude of migration rates. Nevertheless, for the convenience of further analysis, we can obtain compact solutions for some special cases:

(A) $\varepsilon = 0$, the extreme case of two completely *isolated habitats*.

(B) $\varepsilon \to \infty$, the extreme case of *perfectly mixed habitats*.

(C) sufficiently small $\varepsilon << \varepsilon_0$, the case of weakly coupled or *semi-isolated habitats*, where the boundary migration magnitude ε_0 is defined by the condition:

$$\varepsilon_0 = \frac{\min(r_1, r_2, s_1, s_2)}{\max(D_m S_m, D_m, D_n S_n, D_n)}, \qquad \text{(C1)}$$

meaning that maximum migration rate is smaller than minimum growth rate or migration flows do not exceed population growths.

For intermediate range of migration rates, where compact analytical solutions cannot be obtained, we find numerical solutions and check these analytical results.

Also, for an intermediate range of migration rates ($\varepsilon_0 < \varepsilon < \infty$), where compact analytical solutions cannot be obtained, we calculate a numerical solution for the entire range of migration rates and check our analytical results at extreme A, B and C ranges.

2.1 Isolated habitats

In isolated habitats, we can simply combine well-known result for single-patch equilibrium solutions. On one patch, we have four equilibrium solutions: both species are extinct; one of the species is extinct and both species coexist. Therefore, on both patches, the system (1) has 16 (including trivial) equilibrium solutions (Cressman et.al 2004). Of these, 8 solutions describe a situation in which only one species is present in one patch, the other 6 solutions describe a situation in which species coexist in only one patch, one trivial solution, and finally one solution in which species coexist on both patches. Each solution can be represented as vector of equilibrium population sizes of each species on each patch $\mathbf{X_0}(m_1, m_2, n_1, n_2)$, where

$$\mathbf{X}_0(m_1, m_2, n_1, n_2) = \left(\frac{K_1 - \alpha_1 L_1}{1 - \alpha_1 \beta_1}, \frac{K_2 - \alpha_2 L_2}{1 - \alpha_2 \beta_2}, \frac{L_1 - \beta_1 K_1}{1 - \alpha_1 \beta_1}, \frac{L_2 - \beta_2 K_2}{1 - \alpha_2 \beta_2} \right)^T. \qquad (2)$$

The coexistence of two species in both habitats takes place if all components of the vector $\mathbf{X_0}(m_1, m_2, n_1, n_2)$ are greater than zero, which requires the fulfilment of the following necessary conditions: $\alpha_i < (K_i / L_i) < \beta_i^{-1}$ (C2), which means that the ratio of carrying capacities is within a certain range, $\alpha_i \beta_i < 1$ (C3), which means that intraspecific competition is greater than interspecific competition. In the case of migration between habitats, these conditions ensure *local coexistence* (i.e., species can coexist in isolation within each habitat). Hereinafter, we are mostly interested in the migration of locally coexisting species; accordingly, the local coexistence conditions are used throughout the manuscript.

2.2 Perfectly mixed habitats

In this case, we can separate dynamics of the system (1) into fast and slow parts and apply the Tikhonov theorem (Tikhonov, 1952) in the limit $\varepsilon \to \infty$ (**Appendix A**). Given equal habitat interaction coefficients (i.e., $(\alpha_i = \alpha) \wedge (\beta_i = \beta)$) and the same for both species asymmetry coefficients (i.e., $S_m = S_n = S$), we get four asymptotic solutions $(0,0), (M_0, 0), (0, N_0), (M, N)$. The coexistence solution for each species population on each habitat $\mathbf{X}_{\text{inf}}$, total population of each species on both habitats M, N and overall population of both species T is

$$\mathbf{X}_{\mathbf{inf}} = \begin{pmatrix} m_1 \\ m_2 \\ n_1 \\ n_2 \end{pmatrix} = \frac{2}{(1-\alpha\beta)(1+S)} \begin{pmatrix} M_0 - \alpha N_0 \\ (M_0 - \alpha N_0)S \\ N_0 - \beta M_0 \\ (N_0 - \beta M_0)S \end{pmatrix}, \qquad (3)$$

$$\begin{aligned} M &= m_1 + m_2 = (1-\alpha\beta)^{-1}(M_0 - \alpha N_0) \\ N &= n_1 + n_2 = (1-\alpha\beta)^{-1}(N_0 - \beta M_0) \\ T &= M + N = (1-\alpha\beta)^{-1}\left((1-\beta)M_0 + (1-\alpha)N_0\right) \end{aligned}$$

where M_0, N_0 are

$$(M_0, N_0) = \left(\frac{K_1 K_2 (1+S)(r_1 + S r_2)}{2(K_1 r_2 S^2 + K_2 r_1)}, \frac{L_1 L_2 (1+S)(s_1 + S s_2)}{2(L_1 s_2 S^2 + L_2 s_1)} \right). \qquad (4)$$

Note that in the case of symmetric migrations (i.e., $S = 1$), the single species solutions coincide with well-known result for population dynamics in two coupled patches (Freedman and Waltman (1977), Holt (1985), Arditi et. al. (2015)). In addition, we can find changes in equilibrium abundances when the migration magnitude is varied from zero to infinity. In the coexistence case, equation (2) minus equation (3) gives

$$(\Delta M, \Delta N) = (1-\alpha\beta)^{-1}(\Delta M_0 - \alpha \Delta N_0, \Delta N_0 - \beta \Delta M_0), \qquad (5)$$

where $\Delta M_0, \Delta N_0$ are

$$(\Delta M_0, \Delta N_0) = \left(\frac{(K_2 - K_1 S)(K_2 r_1 - K_1 S r_2)}{(K_1 r_2 S^2 + K_2 r_1)}, \frac{(L_2 - L_1 S)(L_2 s_1 - L_1 S s_2)}{(L_1 s_2 S^2 + L_2 s_1)} \right). \qquad (6)$$

Equations (5) and (6) show that equilibrium abundances do not change if one of conditions $K_2 = K_1 S$ (C4) or $\frac{r_1}{SK_1} = \frac{r_2}{K_2}$ (C5) combines with one of conditions $L_2 = L_1 S$ (C6) or $\frac{s_1}{SL_1} = \frac{s_2}{L_2}$ (C7), otherwise, equilibrium abundances may change in any directions depending on conditions. It can be noted that these zero change conditions (ZCC) correspond to the conditions of ideal free distribution (IDF) for each species. A pair of conditions (C4) and (C6) requires equality of effective (i.e., with respects to migration asymmetry) carrying capacities, while a pair of conditions (C5) and (C7) requires equality of effective intraspecific competition in both habitats and no net spillover effect. Also, note that competition between species (i.e., interspecific competition) does not affect ZCC conditions.

Significantly, the conditions for coexistence for isolated habitats (i.e., $\alpha < (K_i / L_i) < \beta^{-1}$) and perfectly mixed habitats (i.e., $\alpha < (M_0 / N_0) < \beta^{-1}$) are structurally different. In the case of isolated habitats, these conditions do not depend on net growth rates, while in the case of mixed habitats, they do. This means that local coexistence does not guarantee *global coexistence* (i.e., coexistence within migration-connected habitats). In **Appendix B**, we explore how coexistence conditions depend on habitat heterogeneity and differences between species.

2.3 Semi-isolated habitats

In case of sufficiently small (C1) migration magnitude (or strong barrier between habitats), we can use the method of perturbation theory and consider ε as a perturbation parameter and find perturbed equilibrium as $\mathbf{X}_\varepsilon = \mathbf{X}_0 + \varepsilon \mathbf{X}_1 + o(\varepsilon^2)$, which is asymptotically stable under common assumptions (Freedman and Waltman 1977) if non-perturbed equilibrium is stable (i.e., stability is preserved for the perturbed equilibrium).

Here, we are primarily interested in the perturbed solution around equilibrium that allows the coexistence of two species in both habitats, i.e., when $\mathbf{X}_0$ is given by equation (2). We now focus on the effect of difference in migration rates between two otherwise equivalent species. This is useful for considering two e.g., genotypes of the same species that differ only in their migration behaviour with potential management implications (see e.g., Andersen et al., 2018; Alós et al., 2019). We will derive their equilibrium populations based on the following simplifications of the general solution (2). (a) We assume that interaction coefficients do not depend on habitat i.e., $\alpha_1 = \alpha_2, \beta_1 = \beta_2$ and they are symmetrical i.e., $\alpha = \beta$; (b) carrying capacities are equal for both species, but may differ among habitats i.e., $K_1 = L_1, K_2 = L_2$. With these specifications, the equilibrium solution (2) reduces to $\mathbf{X}_0(m_1, m_2, n_1, n_2) = \frac{1}{(1+\alpha)}(K_1, K_2, K_1, K_2)^T$. After some calculations (**supplementary material**), we can derive the linear term of the extended solution as:

$$\mathbf{X}_1 = \begin{pmatrix} \dfrac{K_2(D_m s_1 - \alpha D_n r_1) + K_1(\alpha D_n S_n r_1 - D_m S_m s_1)}{r_1 s_1 (1-\alpha^2)} \\ \dfrac{K_2(\alpha D_n r_2 - D_m s_2) + K_1(D_m S_m s_2 - \alpha D_n S_n r_2)}{r_2 s_2 (1-\alpha^2)} \\ \dfrac{K_2(D_n r_1 - \alpha D_m s_1) + K_1(\alpha D_m S_m s_1 - D_n S_n r_1)}{r_1 s_1 (1-\alpha^2)} \\ \dfrac{K_2(\alpha D_m s_2 - D_n r_2) + K_1(D_n S_n r_2 - \alpha D_m S_m s_2)}{r_2 s_2 (1-\alpha^2)} \end{pmatrix}. \qquad (7)$$

Solution (7) can be further simplified if we assume that the net growth rates are the same for both “fast” and “slow” behaviours (i.e., $s_1 = r_1, s_2 = r_2$) and similar migration preferences (i.e., $S_n = S_m \equiv S$) as

$$\mathbf{X}_1 = \frac{SK_1 - K_2}{1-\alpha^2}\left(-\frac{D_m - \alpha D_n}{r_1}, \frac{D_m - \alpha D_n}{r_2}, -\frac{D_n - \alpha D_m}{r_1}, \frac{D_n - \alpha D_m}{r_2} \right)^T . \qquad (8)$$

Based on (8), we can calculate each species population on each habitat $\mathbf{X}_\varepsilon$, total population of each species on both habitats M, N and overall population of both species T as:

$$\mathbf{X}_\varepsilon = \begin{pmatrix} m_1 \\ m_2 \\ n_1 \\ n_2 \end{pmatrix} = \frac{1}{1+\alpha}\begin{pmatrix} K_1 \\ K_2 \\ K_1 \\ K_2 \end{pmatrix} + \varepsilon \frac{(SK_1 - K_2)}{(1-\alpha^2) r_1 r_2}\begin{pmatrix} r_2(\alpha D_n - D_m) \\ r_1(D_m - \alpha D_n) \\ r_2(\alpha D_n - D_m) \\ r_1(D_n - \alpha D_m) \end{pmatrix} + o(\varepsilon^2)$$

$$M = m_1 + m_2 = \frac{(K_1 + K_2)}{1+\alpha} + \varepsilon \frac{(SK_1 - K_2)}{1-\alpha^2}\frac{(r_1 - r_2)}{r_1 r_2}(D_m - \alpha D_n) + o(\varepsilon^2) \qquad (9)$$

$$N = n_1 + n_2 = \frac{(K_1 + K_2)}{1+\alpha} + \varepsilon \frac{(SK_1 - K_2)}{1-\alpha^2}\frac{(r_1 - r_2)}{r_1 r_2}(D_n - \alpha D_m) + o(\varepsilon^2)$$

$$T = M + N = \frac{2(K_1 + K_2)}{1+\alpha} + \varepsilon \frac{(SK_1 - K_2)}{1+\alpha}\frac{(r_1 - r_2)}{r_1 r_2}(D_n + D_m) + o(\varepsilon^2) .$$

The effect of migration on population sizes is summarized in **Table 1**. Evidently, the interaction between environmentally driven conditions (i.e., net growth rates and carrying capacities) and migration behaviours (i.e., migration rates and migration preferences) can cause a wide variety of effects. Both “fast” and “slow” migrating behaviours can be beneficial for species abundance depending on other conditions. Positive correlation between r and K (i.e., $(r_1 > r_2) \wedge (K_1^{eff} > K_2)$) leads to increasing of total population size relative to sum of carrying capacities, where $K_1^{eff} \equiv SK_1$ is effective carrying capacity. Note that in this case ZCC conditions for each species (i.e., $K_1^{eff} = K_2, r_1 = r_2, D_m = \alpha D_n$ and $K_1^{eff} = K_2, r_1 = r_2, D_n = \alpha D_m$) and total population (i.e., $K_1^{eff} = K_2, r_1 = r_2$) are all different.

Based on the results from **Table 1**, we can already highlight three classes of environmental conditions (with respect to evolutionary selection):

(1) *disruptive conditions* under which differences in migration rates are beneficial for both (“fast” and “slow”) behaviours and potentially can lead to divergence of migration behaviour.

(2) *convergent conditions* under which differences in migration rates are beneficial for one type of behaviour only.

(3) *sessile conditions* under which migration leads to a decrease in equilibrium population sizes for both types.

Note that the strength of competition affects the case classification and disruptive conditions take place only for moderate differences in migration rates (i.e., $D_m < \alpha^{-1} D_n$).

2.4 Numerical solution

In previous sections, we have fond analytical solutions for the system (2) at specific ranges of the migration magnitude. In this section, we calculate a numerical solution for the entire range of migration magnitude and compare the numerical and analytical results. The Mathcad program code for the numerical solution of system (2) can be viewed in the supplementary section, as well as can be downloaded from GitHub (https://github.com/Alexander-Sadykov/Migration_two_habitats_two_species/Numerical_solutions_2x2). Here, we consider two ecologically equivalent species (i.e., $r_i = s_i$, $K_i = L_i$ and $\alpha_i = \beta_i = \alpha < 1$) which differ only in migration rate ($D_m > D_n$). Note that under these assumptions, the conditions for local and global coexistence are the same (table B), i.e., locally coexisting populations always coexist globally. Two specific numerical solutions for "disruptive" and "sessile" conditions are shown on **fig.2**. It can be seen that numerical and analytical solutions coincide at $\varepsilon \to 0$ and $\varepsilon \to \infty$, and that at a small magnitude of migration $\varepsilon \ll \varepsilon_0$, the linear approximate solutions are in good agreement with the numerical results. Numerical results show that the relationship between population sizes and migration rate is not always monotonic, for example, in the "disruptive" case (fig. 2B), both species reach their maximum population size at some intermediate values of the migration rate. Numerical solutions for all cases from Table 1 show that at sufficiently high migration rates, the "slow" species always has a larger population size. This observation is consistent with a well-known "*the slower diffuser always prevails*" principle (Dockery et al., 1998, De Angelis et al., 2016). However, full analysis for the entire range of migration rates shows that this principle has limited validity for 2x2 system. Since at low migration rates and positive r-K correlation (grey rows in Table 1), the population of the "fast" species is relatively greater than the population of the "slow" species (e.g., fig.2B).

For locally non-coexisting populations ($\alpha_i = \beta_i = \alpha > 1$), we checked the possibility of global coexistence (i.e., calculated the sign of the maximum eigenvalue of the Jacobin matrix). For the studied set of parameters, asymptotically stable coexisting solutions were not found. Although, for some values of the migration rate, the maximum eigenvalue is close to zero (**fig.3**), which may serve as evidence of "weak global coexistence" (i.e., the characteristic extinction time may be longer than the generation time). In other words, under certain conditions, migration can relax interspecific competition (i.e., reduce the value of the maximum eigenvalue) and slow down the decline to extinction of one the competitor.

3. Model of two competing species on two patches with harvesting on one patch

In this section, we add harvesting pressure to the model (1) to consider the effect of introducing a protected area (e.g., a wildlife reserve or MPA) on the maximum sustainable yield (MSY). Suppose that the first habitat is protected, while the second is harvested with rates C_m and C_n for the species M and N accordingly. We can modify model (1) by including harvest terms as follows:

$$\begin{cases} \dfrac{dm_1}{dt} = r_1 m_1 \left(1 - \dfrac{m_1}{K_1} - \dfrac{\alpha n_1}{K_1}\right) + \varepsilon D_m (m_2 - S_m m_1) \\ \dfrac{dm_2}{dt} = r_2 m_2 \left(1 - \dfrac{m_2}{K_2} - \dfrac{\alpha n_2}{K_2} - \dfrac{C_m}{r_2}\right) + \varepsilon D_m (S_m m_1 - m_2) \\ \dfrac{dn_1}{dt} = s_1 n_1 \left(1 - \dfrac{n_1}{L_1} - \dfrac{\beta m_1}{L_1}\right) + \varepsilon D_n (n_2 - S_n n_1) \\ \dfrac{dn_2}{dt} = s_2 n_2 \left(1 - \dfrac{n_2}{L_2} - \dfrac{\beta m_2}{L_2} - \dfrac{C_n}{s_2}\right) + \varepsilon D_n (S_n n_1 - n_2) \end{cases}. \quad (10)$$

Without migrations ($\varepsilon = 0$) the system (10) has the coexistence equilibrium solution:

$$\mathbf{X}_0 = \begin{pmatrix} \dfrac{K_1 - \alpha L_1}{1 - \alpha\beta} \\ \dfrac{K_2 (r_2 s_2 - C_m s_2) - \alpha L_2 (r_2 s_2 - C_n r_2)}{r_2 s_2 (1 - \alpha\beta)} \\ \dfrac{L_1 - \beta K_1}{1 - \alpha\beta} \\ \dfrac{L_2 (r_2 s_2 - C_n r_2) - \beta K_2 (r_2 s_2 - C_m s_2)}{r_2 s_2 (1 - \alpha\beta)} \end{pmatrix}. \quad (11)$$

Based on the equilibrium (11), we can find the harvest rate vector $\mathbf{C}_{\mathbf{MSY}}(C_n, C_m)$ that provide maximum sustainable yield $\mathbf{H}_{\mathbf{MSY}} = \mathbf{C}_{\mathbf{MSY}}^T \mathbf{X}_{\mathbf{MSY}}$ by solving harvest optimization problem i.e., $\max[\mathbf{C}^T \mathbf{X}_0(\mathbf{C})]$. For instance, in the case of equal carrying capacities $L_i = K_i$ and equal net growth rates $s_i = r_i$, the solution has a simple compact form:

$\mathbf{C}_{\mathbf{MSY}} = \left(\dfrac{r_2(1+\beta)}{\alpha+\beta+2}, \dfrac{r_2(1+\alpha)}{\alpha+\beta+2}\right)^T$, $\mathbf{H}_{\mathbf{MSY}} = \left(\dfrac{r_2 K_2 (1+\beta)}{(\alpha+\beta+2)^2}, \dfrac{r_2 K_2 (1+\alpha)}{(\alpha+\beta+2)^2}\right)^T$. Further, for the simpler case of equal interaction coefficients $\beta = \alpha$, this gives the well-known result $\mathbf{C}_{\mathbf{MSY}} = \left(\dfrac{r_2}{2}, \dfrac{r_2}{2}\right)^T$ and $\mathbf{H}_{\mathbf{MSY}} = \left(\dfrac{r_2 K_2}{4(1+\alpha)}, \dfrac{r_2 K_2}{4(1+\alpha)}\right)^T$.

Approximate solution of the system (10) at sufficiently small migration magnitude can be derived in the same way as for system (1). In this case, the linear approximation term is

$$\mathbf{X}_1 = \begin{pmatrix} -\dfrac{(D_m-\alpha D_n)(K_1Sr_2-K_2(r_2-C))}{r_1r_2(1-\alpha^2)} \\ \dfrac{(D_m-\alpha D_n)(K_1Sr_2-K_2(r_2-C))}{r_2(r_2-C)(1-\alpha^2)} \\ -\dfrac{(D_n-\alpha D_m)(K_1Sr_2-K_2(r_2-C))}{r_1r_2(1-\alpha^2)} \\ \dfrac{(D_n-\alpha D_m)(K_1Sr_2-K_2(r_2-C))}{r_2(r_2-C)(1-\alpha^2)} \end{pmatrix}. \qquad (12)$$

Accordingly, approximate values of MSY harvest rates, MSY harvest of each species and overall harvest for both species can be calculated as:

$$\mathbf{C}_{\mathbf{MSY}} = \left(\frac{r_2}{2},\frac{r_2}{2}\right)^{\mathbf{T}} - \varepsilon\frac{(D_m+D_n)(K_2-4K_1S)}{4K_2}(1,1)^{\mathbf{T}} + o(\varepsilon^2,\varepsilon^2)$$

$$\mathbf{H}_{\mathbf{MSY}} = \frac{r_2K_2}{4(1+\alpha)}(1,1)^{\mathbf{T}} - \frac{\varepsilon(K_2-2K_1S)}{2(1+\alpha)(1-\alpha)}\left(D_m - \alpha D_n, D_n - \alpha D_m\right)^{\mathbf{T}} + o(\varepsilon^2,\varepsilon^2). \qquad (13)$$

$$TH_{MSY} = \frac{r_2K_2}{2(1+\alpha)} - \varepsilon\frac{(D_m+D_n)(K_2-2K_1S)}{2(1+\alpha)} + o(\varepsilon^2)$$

As **Table 2** shows, migration between sites may lead to multidirectional (increasing or decreasing) effects on the MSY harvest, depending on specific values of carrying capacities, migration rates and asymmetry of migration flows. The practical effect is that predicting the ecological consequences is far from simple.

Optimal choice of protected area

In accordance with the resource management goal of maximising harvesting strictly subject to sustainability conditions and seeking a synergy between the two, we examine the prospect for designating a protected area (habitat partition) which can both conserve the population and increase the harvest rate over that of an un-partitioned habitat. In particular, we are trying to find the conditions under which the introduction of protected subareas leads to an increase in the maximum sustainable yield for the entire area. As illustration, let us consider some area A with a total carrying capacity K for both species. Let us also assume that this area is ecologically homogeneous in the sense that the carrying capacity is proportional to the area $K(A) \sim A$, which implies that $K = K_1 + K_2$ for $A = A_1 + A_2$, where A_i are subareas of total area A. Further, we can ask how MSY harvest will change if the first subareas becomes protected from exploitation. We can calculate changes in MSY harvest ΔTH_{MSY} as the difference between TH_{MSY} before ($TH_{MSY} = \frac{r_1K_1 + r_2K_2}{2(1+\alpha)}$) and after (equation (13)) introduction of protected area, and up to second order ε we get

$$\Delta TH_{MSY} = -\left(\frac{r_1K_1}{2(1+\alpha)} + \varepsilon\frac{(D_m+D_n)(K_2-2K_1S)}{2(1+\alpha)}\right). \qquad (14)$$

The first term in equation (14) is always negative and represents the loss of potential yield in the protected subarea; the second term represents net migration from the protected to the harvested subarea and can be either negative or positive (spillover effect). We seek the conditions under which migration flows compensate for potential harvesting losses (i.e., $\Delta TH_{MSY} \geq 0$). The ratio A1/A2 for which these conditions are met is then the optimisation objective for management. In order for ΔTH_{MSY} to be non-negative, two conditions must be met: (1) The second term must be negative, which implies that $K_1 > \frac{K_2}{2S}$; (2) The sum of both terms must be positive, which implies that $K_1 < \frac{K_2}{2S-\gamma}$, where $\gamma = \frac{r_1}{(D_m + D_n)\varepsilon}$.

The first condition means that the protected area must be large enough to ensure a significant migration flow, while the second condition means that the protected area must be small enough not to suppress the harvest. Combining these opposite requirements, we obtain the following inequality for the optimal choice of a protected area:

$$\frac{1}{2S} < \frac{K_1}{K_2} < \frac{1}{2S-\gamma}. \qquad (15)$$

The optimal condition (15) for carrying capacities ratio also represents condition for protected/harvested subareas $\frac{K_1}{K_2} \equiv \frac{A_1}{A_2}$, since we assume a homogeneous environment. The optimal choice solution exists only if $S > \gamma / 2$, taking into account that $\gamma > 1$ for $\varepsilon << r_1$ (linear approximation condition), it can be noted that a high asymmetry of migration flows is required for the optimal choice to exist (**fig.4**). In other words, the protected area must be a strong enough pseudo-source. Also, for $S >> \gamma$, there is approximate solution $A_2 \approx 2SA_1$, or the exploited area should be approximately $2S$ times larger than the protected area.

4. Discussion

The 2x2 (two-species in two habitats) model is a minimal baseline model, which allows the study of mutual relations between competition, migration and coexistence. This enables analytical results to be found, so can contribute to answering some outstanding research questions The relationship between competition and migration can be examined by comparing the previous single-species model (Freedman and Waltman, 1977; Holt, 1985; DeAngelis and Zhang, 2014; Arditi et.al., 2015) with the two-species model with competition.

For a small migration magnitude $\varepsilon << \varepsilon_0$, it is noted that for the total abundance $T = M + N$, the results of both one- and two-species models are mutually consistent, that is, fragmentation (i.e., dividing population on subpopulations) is beneficial for total population size in the case of positive correlation between intrinsic growth rate and effective carrying capacity, while fragmentation is detrimental in the opposite case. Although the overall population size is consistent with the single-species model, the population size of each species may deviate from the single-species model’s prediction. For fast-migrating species, a positive correlation between r and K is always beneficial, but for slow-migrating species, such a correlation may be detrimental in the case of a significant (i.e., $D_m > \alpha^{-1} D_n$) difference between migration rates (**Table 1**). Conversely, a negative correlation between r and K is always detrimental to a fast-migrating species, but in some cases may be beneficial to a slow-migrating species. In general, in a community of two competing species at small migration rates, a fast-migrating species tends to behave as predicted by single-species models, while a slow-migrating species does the opposite. This qualitative observation might be useful in explaining the preferred habitats for competing species with different migratory behaviours. Speculatively: in a competitive environment, migratory species may increase their abundance by occupying rich (i.e., with positive r-K correlation) habitats, whereas sessile species may gain by dwelling in relatively poor (i.e., with negative r-K correlation) habitats, avoiding competition.

If we consider the population sizes of "fast" and "slow" species over the entire range of migration rates, we can see that the well-known principle "*the slower diffuser always prevails*" obtained using continuous models is not fulfilled within the framework of a two-patch model. Although the "slow" species always has a larger population size at high migration rates, the "fast" species may prevail at low migration rates (fig.2B). Thus (in the case of a positive r-K correlation), there is a value of the migration magnitude ε_{ESS} at which the sizes of both populations are equal $M(\varepsilon_{ESS}) = N(\varepsilon_{ESS})$. This value can be called the evolutionarily stable magnitude of the migration rate, since possible mutations in the migration rates will lead to this value.

The relationship between migration and coexistence can be seen in the example of perfectly mixed habitats. The results for this case (**Table B**) show that in a fragmented habitat, the coexistence conditions (B1) may differ from those in a homogeneous environment (C2), and the non-homogeneity of the habitat leads to a dependence of the coexistence conditions on the growth rates. The latter suggests that, depending on the growth rates, migrations can have opposite effects, either ensuring the coexistence of species, or, on the contrary, leading to the extinction of one of the species. In a sense, this is an expected result; nevertheless, (B1) provides a quantitative criterion for different cases.

Finally, the relationship between migration and maximum sustainable yield (MSY) can be examined in the context of conditions for optimal size of wildlife reserve, especially marine protected areas (MPA). In previous works on the optimal MPA size (Hastings and Botsford 1999, Moussaoui and Auger 2015, Takashina 2020), single-species populations having a very high or moderate migration rate were considered. In this manuscript, we examined populations of two competing species at relatively low migration rates. In practical terms, models with a high migration rate are more suitable for describing relatively small (compared to the average migration distance) MPAs, while models with a low migration rate are better suited for describing relatively large MPAs. We have determined the range of parameters for which the optimal MPA size exists. It turned out that the key parameter is the asymmetry of migration flows i.e., an optimal MPA exists if the net migration flow from the protected area exceeds the losses from its non-use for harvesting. We suggest from this that if a fishing ground can be roughly divided into "spawning" and "foraging" areas (i.e., there is strong asymmetry in migration flows between subareas), then the introduction of an MPA over the "spawning" area may be the optimal solution in the sense that it will not reduce the maximum sustainable yield. In practice, it is quite possible that conditions for an optimal MPA cannot be achieved for natural reasons (e.g., there are no behaviourally distinct regions so no significant asymmetry of migration flows). In this case, the deviation from the conditions of the optimal MPA can serve as a convenient indicator for choosing a "next-best" MPA. Although, within the framework of the model, we ignored many biologically important features, showing with a simple case the conditions under which the introduction of the optimal MPA can increase the MSY harvest, we have outlined a benchmark for applied research that takes account of local bio-economic conditions in specific regions.

Acknowledgements

Research supported by Agriculture, Food and the Marine (DAFM) (FishKOSM 487 project, DAFM reference 15/S/744). We also thank the editor and two anonymous reviewers for their careful reading of our first submission and their valuable suggestions.

Appendix A. Equilibrium solution for perfectly mixed habitats.

Rewrite system (1) for fast m_1, n_1 and slow $M = (m_1 + m_2)/2, N = (n_1 + n_2)/2$ variables. Taking into account that $m_2 = 2M - m_1, n_2 = 2N - n_1$), we get couple of equations for fast variables

$$\begin{gathered}\frac{dm_1}{d\tau_m} = \frac{1}{\varepsilon D_m} m_1 r_1 \left(1 - \frac{m_1}{K_1} - \frac{\alpha_1 n_1}{K_1}\right) + (2M - (1+S_m)m_1) \\ \frac{dn_1}{d\tau_n} = \frac{1}{\varepsilon D_n} n_1 s_1 \left(1 - \frac{n_1}{L_1} - \frac{\beta_1 m_1}{L_1}\right) + (2N - (1+S_n)n_1)\end{gathered} \quad , \qquad \text{(A1)}$$

where $\tau_m = \varepsilon D_m t, \tau_n = \varepsilon D_n t$. At $\varepsilon \to \infty$ the first term in each equation can be dropped and fast equations are obtained as

$$\begin{gathered}\frac{dm_1}{d\tau_m} = 2M - (1+S_m)m_1 \\ \frac{dn_1}{d\tau_n} = 2N - (1+S_n)n_1\end{gathered} \quad , \qquad \text{(A2)}$$

which have asymptotically stable solutions:

$$m_1 = \frac{2}{(1+S_m)} M \, , \; n_1 = \frac{2}{(1+S_n)} N \, . \qquad \text{(A3)}$$

After substitution (A3) and letting $S_n = S_m = S$, we get couple of equations for slow variables:

$$\begin{gathered}\frac{dM}{dt} = \frac{M(K_1 K_2 (r_1 + S r_1 + S r_2 + S^2 r_2) - 2(K_2 r_1 + K_1 r_2 S^2)M - 2\alpha(K_2 r_1 + K_1 r_2 S^2)N)}{K_1 K_2 (1+S)^2} \\ \frac{dN}{dt} = \frac{N(L_1 L_2 (s_1 + S s_1 + S s_2 + S^2 s_2) - 2(L_2 s_1 + L_1 s_2 S^2)N - 2\beta(L_2 s_1 + L_1 s_2 S^2)M)}{L_1 L_2 (1+S)^2}\end{gathered} \quad ,$$

which is Lotka-Volterra competition system in its structure and accordingly it has four asymptotic solutions $(0,0), (M_0, 0), (0, N_0), (M, N)$ shown in main text, equations (3) and (4).

Appendix B. Conditions for coexistence in perfectly mixed habitats.

A biologically meaningful solution for the coexistence of competing species exists if both equilibrium populations (3) are positive, i.e., $(\alpha\beta < 1) \wedge ((M_0 / N_0) > \alpha) \wedge ((N_0 / M_0) > \beta)$ which can be rewritten as

$$\alpha < \frac{K_1K_2}{L_1L_2}\frac{(r_1+Sr_2)}{(s_1+Ss_2)}\frac{(L_1s_2S^2+L_2s_1)}{(K_1r_2S^2+K_2r_1)} < \frac{1}{\beta} \ . \qquad \text{(B1)}$$

It can be noted that condition (B1) is quite different from the coexistence condition for isolated habitat, which is $(\alpha < (K_1 / L_1) < \beta^{-1}) \wedge (\alpha < (K_2 / L_2) < \beta^{-1})$. The main feature is that in perfectly mixed habitat, the condition for the coexistence (B1) depends on their growth rates, which is not the case for isolated habitats. In order to understand what specifically affects the change in the coexistence conditions, let us consider two types of transformations in B1: gradual reduction of habitat heterogeneity and reduction of the ecological difference between species. In the first case, let us assume absence of heterogeneity in growth rates $(r_1 = r_2 = r) \wedge (s_1 = s_2 = s)$ and get

$$\frac{K_1K_2}{L_1L_2}\frac{(r_1+Sr_2)}{(s_1+Ss_2)}\frac{(L_1s_2S^2+L_2s_1)}{(K_1r_2S^2+K_2r_1)} \xrightarrow[r_1=r_2,s_1=s_2]{} \frac{K_1K_2}{L_1L_2}\frac{(L_1S^2+L_2)}{(K_1S^2+K_2)} \ , \qquad \text{(B2)}$$

than assume absence of heterogeneity in carrying capacities $(K_1 = K_2 = K) \wedge (L_1 = L_2 = L)$ and get

$$\frac{K_1K_2}{L_1L_2}\frac{(r_1+Sr_2)}{(s_1+Ss_2)}\frac{(L_1s_2S^2+L_2s_1)}{(K_1r_2S^2+K_2r_1)} \xrightarrow[K_1=K_2=K,L_1=L_2=L]{} \frac{K}{L}\frac{(r_1+Sr_2)}{(s_1+Ss_2)}\frac{(s_2S^2+s_1)}{(r_2S^2+r_1)} \ . \qquad \text{(B3)}$$

Note that in the case of equally desirable habitats (i.e., $S = 1$), condition (B3) is the same as the coexistence condition for a single-patch (totally homogeneous) habitat (i.e., $\alpha < (K / L) < \beta^{-1}$). If we simultaneously assume the homogeneity of the growth rate and carrying capacity, then condition (B1) is reduced to 1, which also coincides with the coexistence condition for the single-patch case (i.e., $\alpha\beta < 1$).

In the second case, let us assume species equivalence in growth rates $r_i = s_i$ and get

$$\frac{K_1K_2}{L_1L_2}\frac{(r_1+Sr_2)}{(s_1+Ss_2)}\frac{(L_1s_2S^2+L_2s_1)}{(K_1r_2S^2+K_2r_1)} \xrightarrow[r_1=s_1,r_2=s_2]{} \frac{K_1K_2}{L_1L_2}\frac{(L_1r_2S^2+L_2r_1)}{(K_1r_2S^2+K_2r_1)} \ , \qquad \text{(B4)}$$

than assume species equivalence in carrying capacities $K_i = L_i$ and get

$$\frac{K_1K_2}{L_1L_2}\frac{(r_1+Sr_2)}{(s_1+Ss_2)}\frac{(L_1s_2S^2+L_2s_1)}{(K_1r_2S^2+K_2r_1)} \xrightarrow[K_1=L_1,K_2=L_2]{} \frac{(r_1+Sr_2)}{(s_1+Ss_2)}\frac{(K_1s_2S^2+K_2s_1)}{(K_1r_2S^2+K_2r_1)} \ . \qquad \text{(B5)}$$

For ecologically equivalent species (i.e., $r_i = s_i$ and $K_i = L_i$), condition (B1) is reduces to 1, which again coincides with the coexistence condition for the single-patch case (i.e., $\alpha\beta < 1$).

Table B shows the conditions of existence for various combinations of parameters.

Table B. Coexistence conditions for different levels of species differences and heterogeneity of habitats.

Species differences		αβ<1	B3	B2	B1
	$r_i=s_i$	αβ<1	B3	B2	B4
	$K_i=L_i$	αβ<1	αβ<1	αβ<1	B5
	$(r_i=s_i)$ ∧ $(K_i=L_i)$	αβ<1	αβ<1	αβ<1	αβ<1
		$(K_i=K)\wedge(L_i=L)$ $(r_i=r)\wedge(s_i=s)$	$(K_i=K)\wedge(L_i=L)$	$(r_i=r)\wedge(s_i=s)$	
	Habitat heterogeneity				

The cells for which the coexistence conditions are the same as for the single-patch habitat are marked in grey. The cells for which the conditions of coexistence do not depend on the growth rates are marked in light grey.

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Tables

Table 1. Effect of migrations on equilibrium population sizes under different conditions

Net growth rates (r)	Carrying capacities and migration asymmetry (K, S)	Migration rates (D_m, D_n), where $D_m > D_n$	Sign of effect on population sizes of species M, species N and total population T=M+N, (M, N, T)	Classification of conditions
$r_1 > r_2$	$SK_1 > K_2$	$D_m > \alpha^{-1} D_n$	(+,- ,+)	Convergent
		$D_m < \alpha^{-1} D_n$	(+,+,+)	Disruptive
	$SK_1 < K_2$	$D_m > \alpha^{-1} D_n$	(- ,+, -)	Convergent
		$D_m < \alpha^{-1} D_n$	(- ,- ,-)	Sessile
$r_1 < r_2$	$SK_1 > K_2$	$D_m > \alpha^{-1} D_n$	(- ,+ ,-)	Convergent
		$D_m < \alpha^{-1} D_n$	(- ,- ,-)	Sessile
	$SK_1 < K_2$	$D_m > \alpha^{-1} D_n$	(+ ,- ,+)	Convergent
		$D_m < \alpha^{-1} D_n$	(+ ,+,+)	Disruptive

Cases with a positive correlation between r and K are marked by grey. Note that a positive r-K correlation is always beneficial for the "fast species" and total population, whereas a negative correlation may be beneficial for the "slow species" but always disadvantageous for total population.

Table 2. Effect of migrations on $\mathbf{H}_{\mathbf{MSY}}$ under different habitat conditions

Carrying capacities and migration asymmetry (K, S)	Migration/dispersion rates for species M and N (Dm, Dn)	Sign of effect on Hmsy, for species M, species N and total population, consequently (HMmsy,HNmsy,HTmsy)
$2SK_1 > K_2$	$D_m > \alpha^{-1} D_n$	(+,- ,+)
	$D_m < \alpha^{-1} D_n$	(+,+,+)
$2SK_1 < K_2$	$D_m > \alpha^{-1} D_n$	(- ,+, -)
	$D_m < \alpha^{-1} D_n$	(- ,- ,-)

Figures

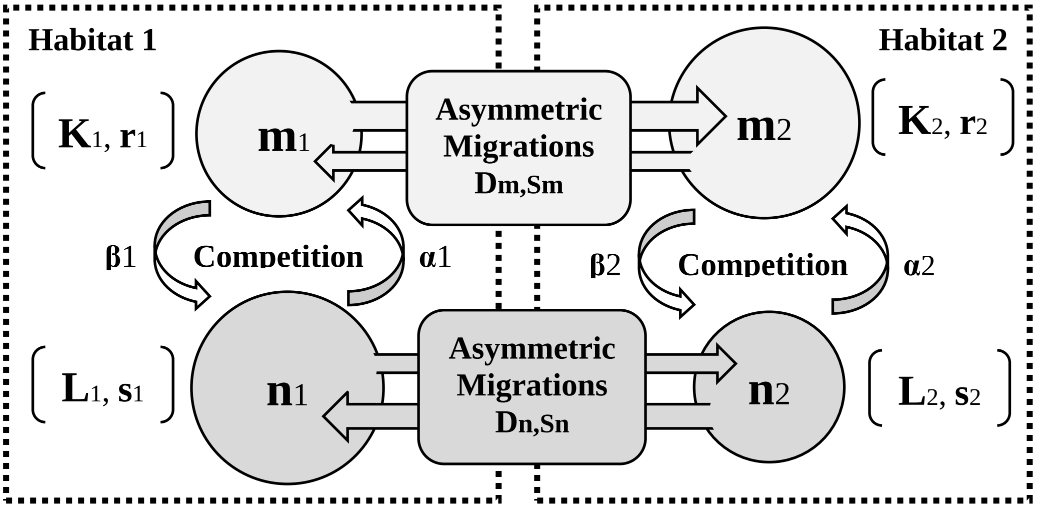

Fig.1 Structural components of the model of two competing species migrating between two habitats.

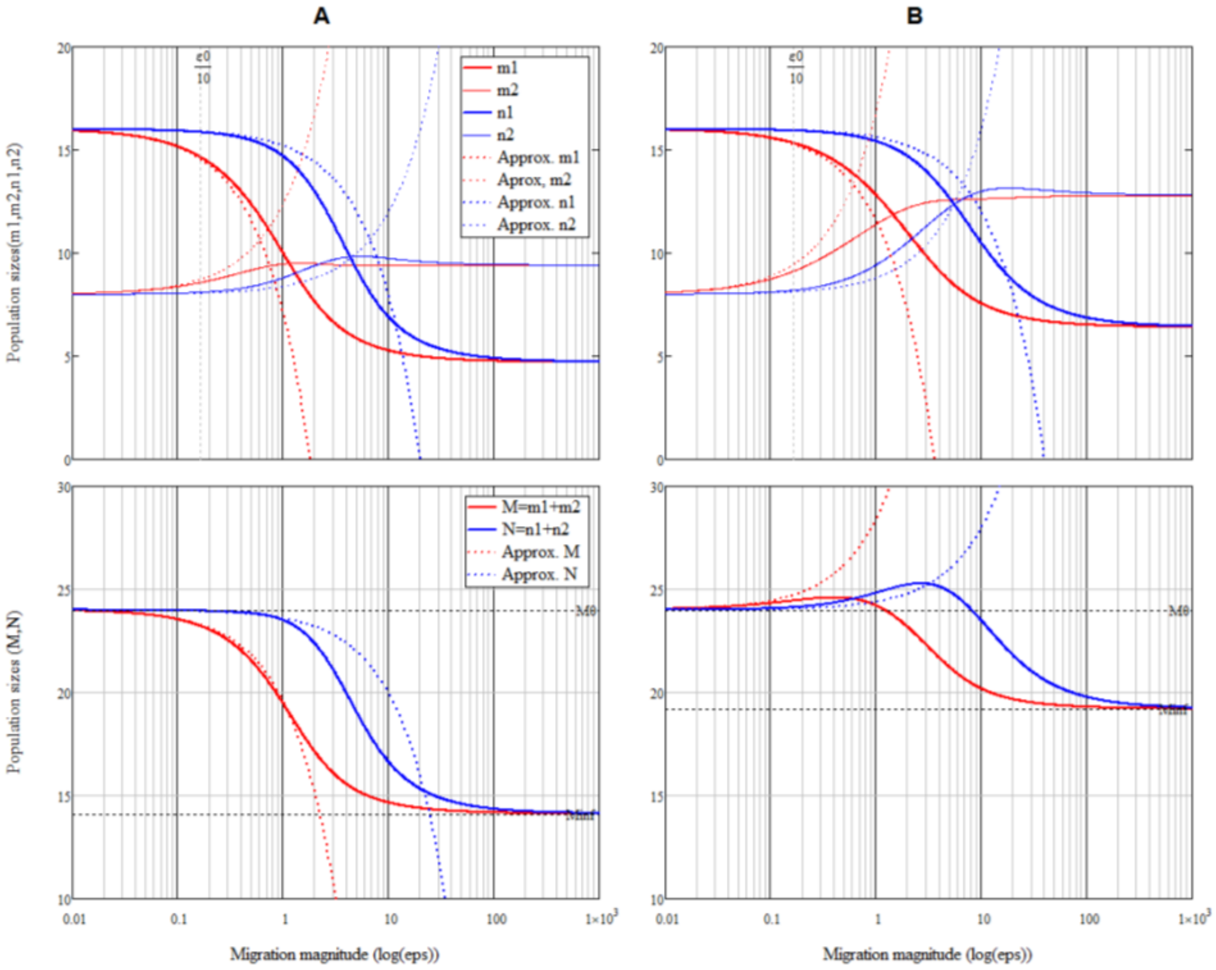

Fig.2 Population sizes depending on the log magnitude of the migration rate under "sessile" (A) and "disruptive" (B) conditions. The top plots show the population sizes of each species in each habitat (red lines for "fast" and blue for "slow" species). The bottom plots show the total population sizes for both species. Blue and red dotted lines show linear approximate solutions (equation 9). Black vertical dashed lines mark the boundary value of the migration magnitude ($\varepsilon \le 0.1 \cdot \varepsilon_0$), up to which the linear approximation gives a good fit. Black horizontal dashed lines mark analytical solutions of system (1) in the cases $\varepsilon = 0$ and $\varepsilon \to \infty$ as M_0 and M_{inf} respectively. Parameters for the "sessile" case are $r_1 = 1, r_2 = 2$, parameters for the "disruptive" case are $r_1 = 2, r_2 = 1$, other parameters are $K_1 = 20, K_2 = 10, D_m = 0.3, D_n = 0.1, \alpha = 0.25, S = 2$.

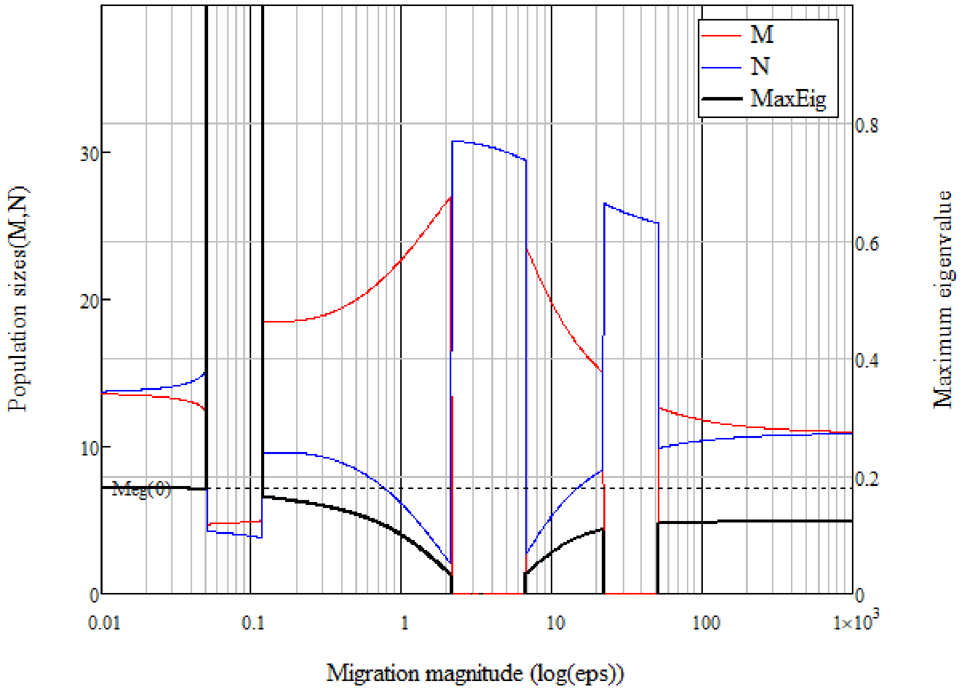

Fig.3 Total population sizes and the maximum eigenvalue of the Jacobian matrix depending on the log magnitude of the migration rate for locally non-coexisting populations (red lines for "fast" and blue for "slow" species). Sharp steps represent regime switching from unstable coexistence to extinction of one of the species. $Meg(0)$ is value of the maximum eigenvalue in the absence of migration. The interspecific competition coefficient is $\alpha = 1.25$, other parameters are $r_1 = 2, r_2 = 1, K_1 = 20, K_2 = 10, D_m = 0.3, D_n = 0.1, S = 2$.

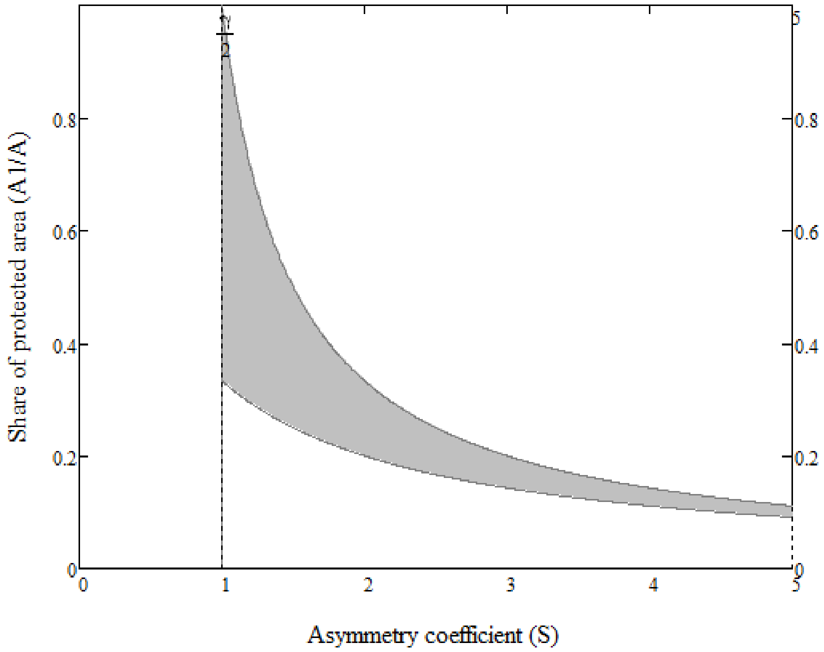

Fig.4 Conditions for optimal choice of protected area (shaded domain). The vertical axis shows the relative share of the protected area (A_1 / A), the horizontal axis shows the coefficient of asymmetry S. The picture is shown at $\gamma = 2$. It can be noted that the optimal choice solution does not exist at $S \le \gamma / 2$, and also that for sufficiently large asymmetry coefficient S, the protected area can be approximated as $A_1 \approx \dfrac{1}{2S+1} A$.