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IMPACT OF GENERALIZED GROWTH DYNAMICS AND SPATIAL DISPERSAL ON MAXIMUM SUSTAINABLE YIELD IN HARVESTED POPULATIONS

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ABSTRACT. This study explores the influence of generalized growth rates on the Maximum Sustainable Yield (MSY) in harvested populations. By employing generalized logistic models, such as the Richards and Gompertz formulations, we analytically derive the conditions under which MSY is attained in single-species systems. The analysis is then extended to multi-patch environments with inter-patch dispersal to examine the impact of migration on total MSY. Our key findings show that the MSY in a connected system is always less than or equal to the sum of the MSYs of isolated patches. Moreover, under biologically realistic assumptions, we demonstrate that increasing migration rates between patches leads to a strictly decreasing total MSY. Numerical simulations support the theoretical results, emphasizing that species-specific growth dynamics and spatial connectivity must be jointly considered for effective resource management. These results reveal a fundamental trade-off between ecological connectivity and harvesting potential in spatially structured populations.

CONTENTS

Key words and phrases. Population Dynamics, Fishery Models, Maximum sustainable yields, resource management, Schaefer model, Generalized Growth Rate, Dispersal.

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1. **Introduction.** The growth and dynamics of populations are influenced by a multitude of factors, among which dispersal plays a critical role. Dispersal, which can occur in varying amounts and often in random patterns, has significant implications for ecosystems. It can disrupt ecological balances, influence the persistence or extinction of species, and reshape the structure of communities. The importance of dispersal in population dynamics has been extensively studied, with foundational insights provided by Allen in works such as [1, 2, 3] and further explored by Holt in [44]. These studies highlight the complex interplay between dispersal and ecosystem stability, offering valuable perspectives on how movement patterns affect ecological outcomes.

In [1], Allen considered the n-patch general model given by the following equations:

$$\frac{dx_i}{dt} = x_i\left(a_i - b_i x_i\right) + \varepsilon \Upsilon_i(x), \quad i = 1,\ldots,n, \tag{1.1}$$

where a_i and b_i are positive constants; $x = (x_1,\ldots,x_n)^T$, where x_i represents the population density in the i-th patch. The parameter ε is the dispersal rate. The function Υ_i represents one of three different mechanisms. The mechanism for linear diffusion is given by:

$$\Upsilon_i(x) = \sum_{j=1, j\neq i}^{n} D_{ij}\left(x_j - \alpha_{ij} x_i\right), \quad , i = 1,\ldots,n, \tag{1.2}$$

where D_{ij} and α_{ij} are positive constants. Dispersal by linear diffusion implies that the species is able to move to all locations within its environment with equal probability. The mechanism for biased diffusion is given by:

$$\Upsilon_i(x) = \sum_{j=1, j\neq i}^{n} D_{ij} x_i\left(x_j - \alpha_{ij} x_i\right), \quad , i = 1,\ldots,n, \tag{1.3}$$

Note that the term "biased" means that the diffusion rate is a function of population density. The diffusion rate is regulated by population density, increasing for large populations and decreasing for small populations. The third type of mechanism is the directed diffusion, which was formulated by Gurney and Nisbet [42], and is given by:

$$\Upsilon_i(x) = \sum_{j=1, j\neq i}^{n} D_{ij}\left(x_j^2 - \alpha_{ij} x_i^2\right), \quad , i = 1,\ldots,n, \tag{1.4}$$

Dispersal by directed diffusion implies that individuals move from regions of high population density to regions of low density, i.e., movement is a function of species density. For more details on the biological interpretation and the continuous formulation of such types of diffusion, we refer the reader to [1]. One particularly interesting case of system (1.1) is that of *perfect mixing*, which occurs when the migration rate ε tends to infinity—in other words, when there are no constraints on movement (see [20, 21, 22, 23, 24, 25, 26, 27, 28, 29] for further examples and details).

The objective of the work by Allen [1] is to study the effect of different types of dispersal on the persistence and extinction of species. The persistence and extinction behavior is completely determined in the two-patch model (1.1)(1.2) for $n = 2$ (see Theorem 1 in [1]). For model (1.1)(1.3), Allen [1, Theorem 2] showed that a population subject to biased diffusion is always persistent and, in fact, represents a strongly persistent population. For more details on persistence and extinction results, see Theorem 3 of [1] for the n-patch

model (1.1)(1.3), Theorem 4 of [1] for the n-patch model (1.1)(1.4), and Proposition 1 of [1] for the two-patch case.

Dispersal plays a crucial role in population dynamics, influencing both local population densities and overall resource availability. In a multi-patch fishery model, individuals migrate between patches in response to ecological factors such as resource abundance, environmental conditions, and intra-specific competition. While migration can enhance population persistence and resilience, it may also lead to unintended consequences for yield optimization. Therefore, understanding how dispersal patterns influence the maximum sustainable yield (MSY) is essential for the development of effective fisheries management strategies.

Most recent mathematical models take into account the spatial distribution of fisheries to study the management of multi-patch systems [5, 11, 43, 50, 51, 52], as well as prey–predator models in a multi-patch environment [31, 53], and Gradostat models [32]. One fundamental principle in fisheries management is the concept of the maximum sustainable yield (MSY), which refers to the largest amount of fish that can be harvested from a population without compromising its long-term sustainability. Determining MSY is key to achieving the objective of harvesting as many fish as possible without risking population collapse [15].

There is considerable interest in understanding how spatial heterogeneity influences the MSY of multi-site systems connected through dispersal or migration. This raises a central question: how does connectivity among fishing sites affect fishery productivity? For instance, can the MSY of a fishery be increased by linking fishing sites through migratory flows—and if so, to what extent does heterogeneity play a role?

The answer is not straightforward. In the case of two fishing sites connected by rapid migrations and focusing on a single harvested species, the MSY of the connected system does not exceed the sum of the MSYs of the isolated sites. However, in a prey–predator context, where the predator is a commercially harvested species and the prey is unharvested, the situation is different. In this case, the MSY of the predator in the connected system can indeed exceed the sum of the MSYs obtained when the two sites are managed independently.

This phenomenon can be summarized as follows:

$$MSY(\varepsilon \to \infty) > MSY_1(\varepsilon \to 0) + MSY_2(\varepsilon \to 0).$$

This result was first established in [4] for a system consisting of two fishing sites connected by fast migration, and is described by the following model:

$$\begin{cases} \dfrac{dx_1}{d\tau} = \varepsilon \left[r_1 x_1 \left(1 - \dfrac{x_1}{K_1}\right) - E x_1 \right] + \gamma_{12} x_2 - \gamma_{21} x_1, \\ \dfrac{dx_2}{d\tau} = \varepsilon \left[r_2 x_2 \left(1 - \dfrac{x_2}{K_2}\right) - E x_2 \right] + \gamma_{21} x_1 - \gamma_{12} x_2, \end{cases} \tag{1.5}$$

where $\varepsilon \to 0$. Furthermore, we also refer to the work [14], in which this result was extended to the case of a single species with variable fishing effort in a multi-site fishery involving an arbitrary number of sites (not limited to two). In this latter study, since the fishing effort is variable, the optimization of the harvest is carried out under a cost constraint, assuming identical fishing operating costs across all sites.

In 2025, Pierre et al. [6] considered a multi-site fishery model with a single harvested fish species and site-specific fishing efforts, described by the following system:

$$\frac{dx_i}{dt} = \varepsilon\left(r_i x_i\left(1-\frac{x_i}{K_i}\right) - qE_i x_i\right) + \sum_{j=1, j\neq i}^{n} (\gamma_{ij}x_j - \gamma_{ji}x_i), \qquad i = 1, \cdots, n. \tag{1.6}$$

For this model, they showed that the Maximum Sustainable Yield (MSY) of the multi-site network, when the sites are connected, is always less than or equal to the sum of the MSYs of the isolated sites. Equality occurs when the fish population is spatially distributed according to the Ideal Free Distribution (IFD), i.e.,

$$MSY(\varepsilon \to \infty) \leq MSY_1(\varepsilon \to 0) + \ldots + MSY_n(\varepsilon \to 0).$$

Recently, Elbetch et al. [33] have generalized these results for all migration rates ε, i.e. they showed that the Maximum Sustainable Yield of the multi-site network is always less than or equal to the sum of the MSYs of the isolated sites for all rate of migration, i.e.,

$$MSY(\varepsilon) \leq MSY_1(\varepsilon \to 0) + \ldots + MSY_n(\varepsilon \to 0), \quad \forall \varepsilon \geq 0.$$

The objective of the present work is to investigate the influence of generalized growth rates on the Maximum Sustainable Yield (MSY) in population dynamics, focusing on both single-species and multi-patch models with harvesting. The study aims to derive conditions for equilibrium stability and to obtain expressions for MSY under various growth models, including logistic, Richards, and Gompertz formulations, in order to understand how different intrinsic growth functions and harvesting efforts affect sustainable yields.

Furthermore, the analysis is extended to multi-patch environments where dispersal between patches is considered, to explore how spatial connectivity and migration influence yield optimization. The theoretical results demonstrate that the total MSY in connected patches is always less than or equal to the sum of MSYs from the isolated patches, regardless of migration intensity. These conclusions are supported by numerical simulations, which illustrate the trade-offs between connectivity and sustainable harvesting.

The structure of this paper is organized as follows: The introduction provides an overview of various studies on single-species and multi-patch models, including population dynamics in connected patches and the concept of Maximum Sustainable Yield (MSY). Section 2 presents fundamental results on the generalized logistic equation with harvesting and derives conditions for MSY. Section 3 examines specific growth models (logistic, Richards, Gompertz) and their MSY calculations. Section 4 extends the analysis to multi-patch environments, comparing MSY between connected and isolated patches, and investigates how migration rates affect total yield at MSY. Section 5 presents numerical simulations validating the theoretical findings. Finally, Section 6 summarizes the key insights, emphasizing the trade-off between connectivity and sustainable yield, and discusses implications for ecological resource management.

2. Generalized growth rate and MSY.

In this section, our goal is to prove several results concerning the generalized logistic equation with harvesting. Let us consider the single-species generalized logistic equation with harvesting, given by:

$$\frac{dx}{dt} = x\varphi(x) - Ex, \tag{2.1}$$

where E denotes the fishing effort, x represents the population density of the species, and $x\varphi(x)$ corresponds to the specific growth rate of the population. Since the specific growth rate may depend on the environment, we list the following hypotheses, which are standard in single-species models (see [35, 58]):

H1. All solutions of the initial value problem (2.1) exist, are unique, and can be continued for all positive times.

H2. $\varphi(0) > 0$, $\frac{d\varphi}{dx}(x) < 0$, there exists $K > 0$ such that $\varphi(K) = 0$, and $x\varphi(x) \to -\infty$ as $x \to +\infty$.

The generalized logistic growth model (2.1) with constant harvesting has two equilibria: $x^* = 0$ and $x^* = x^*(E)$ satisfying $\varphi(x^*(E)) = E$. Note that since φ is strictly decreasing, the equation $\varphi(x) = E$ has a unique solution if and only if $E < \varphi(0)$. The equilibrium $x^*(E)$, which is positive when $E < \varphi(0)$, is stable, while the trivial equilibrium $x^* = 0$ is unstable in this case. Otherwise, when $E \geq \varphi(0)$, the equilibrium $x^* = 0$ is stable.

Remark 1. *As the function φ is strictly decreasing then the function $E \mapsto x^*(E)$ is also strictly decreasing, i.e $\frac{dx^*}{dE}(E) < 0$ for all $0 < E < \varphi(0)$.*

At the positive equilibrium, the harvesting rate is:

$$Y^*(E) = Ex^*(E) = \begin{cases} x^*(E)\varphi(x^*(E)) & if \quad E < \varphi(0), \\ 0 & else. \end{cases} \tag{2.2}$$

The derivative of yield $Y^*(E)$ with respect to the fishing effort E is given by:

$$\frac{dY^*}{dE}(E) = E\frac{dx^*}{dE}(E) + x^*(E) =: \phi(E).$$

Therefore, $\frac{dY^*}{dE}(E) = 0$ if and only if $\phi(E) = 0$. We have $\phi(0) = x^*(0) = K > 0$ and $\phi(\varphi(0)) = \varphi(0)\frac{dx^*}{dE}(\varphi(0)) < 0$ and the function ϕ is continuous so there is at least E^*_{MSY} such that $\phi(E^*_{MSY}) = 0$. Hence, Y^* having a maximum for fishing effort E^*_{MSY} such that $x^*_{MSY} = x^*(E^*_{MSY})$, and corresponding to the *Maximum Sustainable Yield* (MSY). The corresponding yield Y^*_{MSY} is given by the following expression:

$$Y^*_{MSY} = E^*_{MSY}x^*_{MSY} = x^*(E^*_{MSY})\varphi(x^*(E^*_{MSY})). \tag{2.3}$$

Which can rewritten as follow:

$$Y^*_{MSY} = \max_{0 \leq x \leq K} x\varphi(x). \tag{2.4}$$

3. Some examples.

In this section, we provide examples of growth rates: the logistic model, the Richards model, and the Gompertz model. For each model, we calculate the Maximum Sustainable Yield (MSY). We begin by outlining some key properties of these models.

The Gompertz model is characterized by its asymmetric growth curve, which makes it particularly useful for describing phenomena such as tumor growth, where the growth rate gradually slows down over time. Its formula is given by

$$x(t) = K \cdot e^{-\ln\left(\frac{K}{x_0}\right)\cdot e^{-rt}},$$

where K represents the carrying capacity (maximum population size), x_0 is the initial population size, and r is the intrinsic growth rate. The Gompertz model is more flexible than the logistic model for describing asymmetric growth patterns, but it is less intuitive and slightly more complex to fit to data.

The logistic model, on the other hand, is widely used to describe population growth in environments with limited resources. Its formula is given by

$$x(t) = \frac{K}{1 + \left(\frac{K - x_0}{x_0}\right) \cdot e^{-rt}},$$

where the parameters K, x_0, and r have the same meanings as in the Gompertz model. The logistic model produces a symmetric S-shaped (sigmoidal) curve with a clear inflection point, making it simple and intuitive to use. However, its assumption of symmetry around the inflection point limits its flexibility for modeling asymmetric growth patterns.

The Richards model generalizes the logistic model by introducing an additional shape parameter μ, which controls the asymmetry of the growth curve. Its formula is given by

$$x(t) = \frac{K}{\left(1 + \left(\frac{K-x_0}{x_0}\right) \cdot e^{-rt}\right)^{\frac{1}{\mu}}}.$$

This added parameter allows the Richards model to describe a wider range of growth patterns, including asymmetric curves, making it highly flexible. When $\mu = 1$, the Richards model reduces to the logistic model, highlighting its broader applicability. However, this flexibility comes at the cost of increased complexity in parameter estimation and model fitting.

In summary, the Gompertz model is well-suited for asymmetric growth patterns, such as tumor growth, while the logistic model is ideal for simpler, symmetric population growth scenarios. The Richards model offers the greatest flexibility, accommodating a variety of growth shapes, but is more complex to work with due to its additional parameter. The choice of model depends on the specific characteristics of the data and the phenomenon being studied.

Example 1. *Let us consider the single-species logistic equation with harvesting* [54]*:*

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - Ex, \tag{3.1}$$

where r is the growth rate, K the carrying capacity, and E the fishing effort. We now aim to choose the harvesting effort E in order to maximize the total harvesting term. The logistic growth equation (3.1) *with constant harvesting has two equilibria:* $x = 0$ *and*

$$x^*(E) = K\left(1 - \frac{E}{r}\right),$$

which is positive when $E < r$*. When* $x^*(E) > 0$*, it is stable and the trivial equilibrium* $x^* = 0$ *is unstable; otherwise,* $x^* = 0$ *is stable. At the positive equilibrium, the harvesting rate is:*

$$Y^*(E) = Ex^*(E) = \begin{cases} EK\left(1 - \frac{E}{r}\right) & if \qquad E < r, \\ 0 & otherwise. \end{cases} \tag{3.2}$$

The yield $Y^*(E)$ *is a negative parabola with respect to the fishing effort E, having a maximum for* $E^*_{MSY} = \frac{r}{2}$ *corresponding to the MSY. The corresponding value of the stable non-trivial positive equilibrium* x^* *reads as follows:*

$$x^*_{MSY} := x^*(E^*_{MSY}) = \left(1 - \frac{E^*_{MSY}}{r}\right)K = \frac{K}{2}. \tag{3.3}$$

And the corresponding yield Y^*_{MSY} *is given by the following expression:*

$$Y^*_{MSY} = E^*_{MSY}x^*_{MSY} = E^*_{MSY}K\left(1 - \frac{E^*_{MSY}}{r}\right) = \frac{rK}{4}. \tag{3.4}$$

On other hand, using (2.4) *we obtain:*

$$Y^*_{MSY} = \max_{0\le x\le K} x\varphi(x) = \max_{0\le x\le K} rx\left(1 - \frac{x}{K}\right) = \frac{rK}{4}.$$

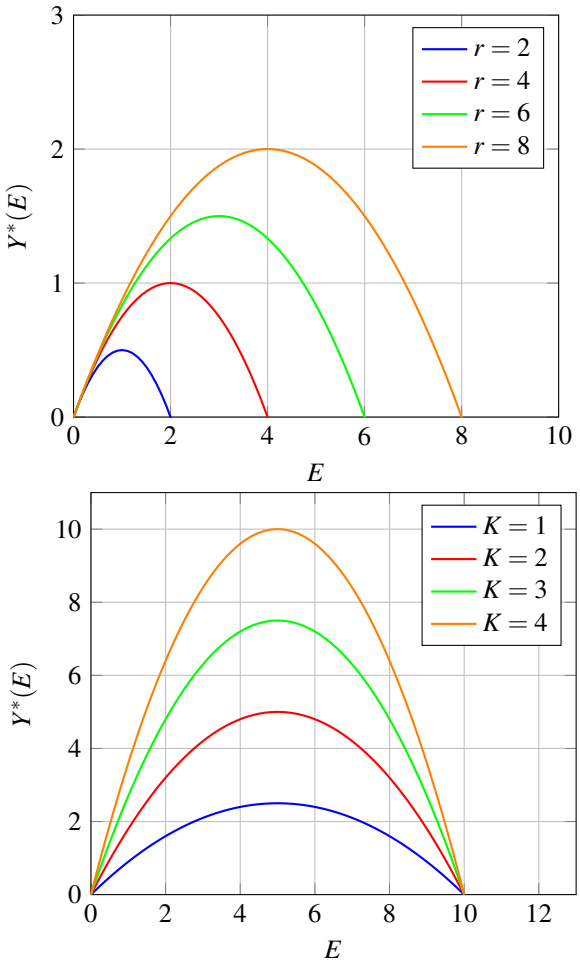


FIGURE 1. The function $Y(E) = EK\left(1 - \frac{E}{r}\right)$ for some values of r and K.

Example 2. *Let us consider the single-species generalized logistic equation (model of Richards* [22, 55]*) with harvesting given by:*

$$\frac{dx}{dt} = rx\left[1 - \left(\frac{x}{K}\right)^{\mu}\right] - Ex, \tag{3.5}$$

where r is the growth rate, K the carrying capacity, μ is a positive number, and E the fishing effort. We are now going to choose the harvesting effort E in order to maximize the total harvesting term. The generalized logistic growth (3.5) with constant harvesting has two equilibria: $x^* = 0$ and $x^*(E) = K\left(1 - \frac{E}{r}\right)^{\mu^{-1}}$, which being positive when $E < r$. When $x^*(E) > 0$, it is stable and the trivial equilibrium $x^* = 0$ is unstable and otherwise $x^* = 0$ is stable. At the positive equilibrium, the harvesting rate is:

$$Y^*(E) = Ex^*(E) = \begin{cases} EK\left(1 - \frac{E}{r}\right)^{\mu^{-1}} & if \quad E < r, \\ 0 & else. \end{cases} \tag{3.6}$$

The yield $Y^*(E)$ having a maximum for $E^*_{MSY} = \frac{\mu}{\mu+1} r$ corresponding to the MSY, see figure 2. The corresponding value of the stable non-trivial positive equilibrium x^* reads as follows:

$$x^*_{MSY} := x^*(E^*_{MSY}) = \left(1 - \frac{E^*_{MSY}}{r}\right)^{\mu^{-1}} K = \left(\frac{1}{\mu+1}\right)^{\mu^{-1}} K. \tag{3.7}$$

And the corresponding yield Y^*_{MSY} is given by the following expression:

$$Y^*_{MSY} = E^*_{MSY} x^*_{MSY} = E^*_{MSY} K \left(1 - \frac{E^*_{MSY}}{r}\right)^{\mu^{-1}} = \mu \left(\frac{1}{\mu+1}\right)^{\mu^{-1}+1} rK. \tag{3.8}$$

On other hand, using (2.4) we obtain:

$$Y^*_{MSY} = \max_{0\le x\le K} x\varphi(x) = \max_{0\le x\le K} rx\left[1 - \left(\frac{x}{K}\right)^{\mu}\right] = \mu \left(\frac{1}{\mu+1}\right)^{\mu^{-1}+1} rK.$$

Note that, the function $\mu \mapsto Y^*_{MSY}(\mu)$ is increasing, indeed, its derivative is given by:

$$\frac{dY^*_{MSY}}{d\mu}(\mu) = -2\left((\mu+1)^{-1}\right)^{\frac{\mu+1}{\mu}} \ln\left((\mu+1)^{-1}\right) \mu^{-1},$$

which is positive for all $\mu > 0$. For $\mu = 1$, the yield value is the MSY is achieved when the fishing effort E is chosen to be equal to half of the growth rate r of the harvested population, and the yield Y^*_{MSY} is becomes $\frac{rK}{4}$ (see also [54]).

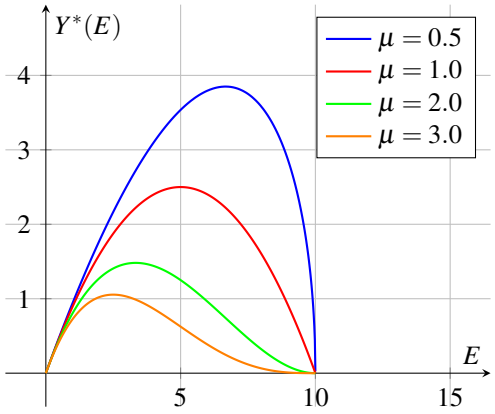


FIGURE 2. Function $Y^*(E)$ for different values of μ

Example 3. *Let us consider the Gompertz equation with harvesting, which is used to describe growth that slows down in a logarithmic manner (see [54]). It is often applied in tumor biology and demography. The differential equation is:*

$$\frac{dx}{dt} = rx \ln\left(\frac{K}{x}\right) - Ex, \tag{3.9}$$

where r is the growth rate, K the carrying capacity, and E the fishing effort. This model captures rapid initial growth followed by a gradual slowdown as the population approaches the carrying capacity K. It is particularly useful for modeling systems in which growth decelerates over time, such as tumor growth or population dynamics.

The Gompertz growth equation (3.9) with constant harvesting has two equilibria: $x = 0$ and $x^*(E) = Ke^{-\frac{E}{r}}$, which is positive for all values of E. At this equilibrium, the harvesting rate is:

$$Y^*(E) = Ex^*(E) = KEe^{-\frac{E}{r}}. \tag{3.10}$$

The derivative of the yield $Y^*(E)$ with respect to the fishing effort E is given by:

$$Y'(E) = K \cdot e^{-\frac{E}{r}} \left(1 - \frac{E}{r}\right)$$

Thus, the yield having a maximum for $E^*_{MSY} = r$ corresponding to the MSY. The corresponding value of the stable non-trivial positive equilibrium x^* reads as follows:

$$x^*_{MSY} := x^*(E^*_{MSY}) = \frac{K}{e}. \tag{3.11}$$

And the corresponding yield Y^*_{MSY} is given by the following expression:

$$Y^*_{MSY} = E^*_{MSY} x^*_{MSY} = \frac{rK}{e}. \tag{3.12}$$

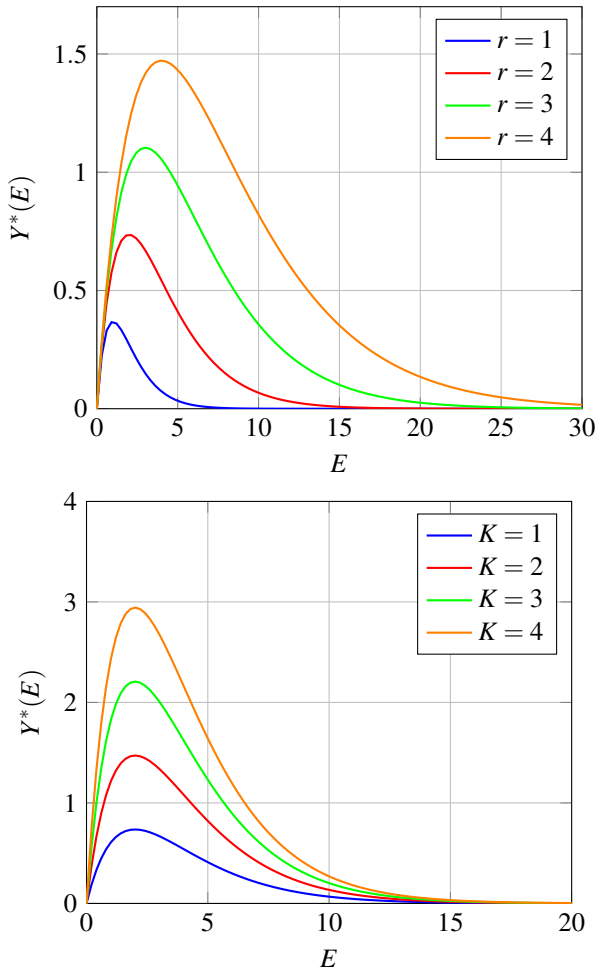


FIGURE 3. The function $Y^*(E) = EKe^{-\frac{E}{r}}$ for some values of r and K.

4. **Multi-patch case.** Let us consider the growth of a single species that can disperse among n patches, described by:

$$\frac{dx_i}{dt} = x_i\varphi_i(x_i) - E_i x_i + \varepsilon \sum_{j=1, j\neq i}^{n} (\gamma_{ij} h_j(x_j) - \gamma_{ji} h_i(x_i)), \qquad i = 1, \ldots, n, \tag{4.1}$$

where E_i are the fishing efforts. The terms $E_i x_i$ represent the Schaefer catch on patch i (see [56]), x_i denotes the population density of the species in the i-th patch, and $\varphi_i(x_i)$ is the specific growth rate of the population in the i-th patch. Since the specific growth rate may depend on the environment of each patch, the function $\varphi_i(x_i)$ is assumed to differ between patches.

The second term on the right-hand side of equation (4.1) describes the diffusion effect between patches, where ε is the migration rate, and $\gamma_{ij} \geq 0$ for all $i \neq j$ represents the asymmetric migration rate, describing the flow of individuals from patch j to patch i. The function $h_i(x_i)$ denotes the rate of dispersal out of the i-th habitat. These rates may, for example, depend on the distance between patches.

We list the following hypotheses, the first two of which are standard in single-species models (see [35, 58]):

H1. All solutions of the initial value problem (4.1) exist, are unique and are continuable for all positive time.

H2. $\varphi_i(0) > 0$, $\frac{d\varphi_i}{dx_i}(x_i) < 0$, there exist $K_i > 0$ such that $\varphi_i(K_i) = 0$ and $x_i\varphi_i(x_i) \to -\infty$ as $x_i \to +\infty$ for all $i = 1, \ldots, n$.

H3. $h_i(0) = 0, \nu_i \geq h_i'(x_i) \geq h_i'(0) > 0$ for all $i = 1, \ldots, n$.

H4. The matrix $\Gamma := (\gamma_{ij})$ where

$$\gamma_{ii} = -\sum_{j=1, j\neq i}^{n} \gamma_{ji} \tag{4.2}$$

is irreducible.

In Hypothesis H2, K_i denotes the carrying capacity of the i-th patch. All patches are considered source patches since $\varphi_i(0) > 0$ for all i.

Hypothesis H3 states that the rate of dispersal out of the i-th patch is density-dependent and increases with the population size in that patch. The requirement is mainly technical, and ν_i represents an upper bound on the growth rate of $h_i(x_i)$.

In Hypothesis H4, the irreducibility of the matrix Γ implies that the set of patches cannot be partitioned into two non-empty disjoint subsets I and J such that there is no migration between a patch in I and a patch in J. That is, the irreducibility of Γ ensures that every patch in system (4.1) is connected via migration, meaning the species can reach any patch i from any other patch j through a sequence of migrations.

In the two-patch case, the matrix Γ is irreducible if and only if both $\gamma_{12} > 0$ and $\gamma_{21} > 0$.

The functions $\varphi_i(x_i)$ and $h_i(x_i)$ play a crucial role in determining the dynamics of the system. Below are some examples that satisfy Hypotheses H2 and H3, respectively.

- Logistic Growth:$\varphi_i(x_i) = r_i\left(1 - \frac{x_i}{K_i}\right)$, where $r_i > 0$ is the intrinsic growth rate and $K_i > 0$ is the carrying capacity. This function satisfies H2 because:$\varphi_i(0) = r_i > 0, \frac{d\varphi_i}{dx_i}(x_i) = -\frac{r_i}{K_i} < 0$, $\varphi_i(K_i) = 0$, and $x_i\varphi_i(x_i) \to -\infty$ as $x_i \to +\infty$.
- Linear Migration: $h_i(x_i) = m_i x_i$, where $m_i > 0$ is the migration rate coefficient. This function satisfies H3 because: $h_i(0) = 0$ and $h_i'(x_i) = m_i > 0$.
- Saturating Migration (Michaelis-Menten Type):$h_i(x_i) = \frac{m_i x_i}{a_i + x_i}$, where $a_i > 0$ is the half-saturation constant. This function satisfies H3 because: $h_i(0) = 0$ and $h_i'(x_i) = \frac{m_i a_i}{(a_i + x_i)^2} > 0$.

4.1. **The total yield at MSY of connected and isolated fishing patches.** Assume that $E_i \leq \varphi_i(0)$ for all i, then according to [27], the model (4.1) has a unique positive equilibrium point in the positive cone $\mathbb{R}^n_+ \setminus \{0\}$. In all of this work, the positive equilibrium of the system (4.1) is denoted by

$$\mathbb{E}^*_n(\varepsilon; E_1, \ldots, E_n) = (x_1^*(\varepsilon; E_1, \ldots, E_n), \ldots, x_n^*(\varepsilon; E_1, \ldots, E_n)),$$

which depends on migration rate ε and fishing efforts of all patches.

The components $x_i^*(\varepsilon; E_1, \ldots, E_n), i = 1, \ldots, n$ of the equilibrium $\mathbb{E}^*_n$ satisfied to the following equations:

$$\begin{aligned} x_i^*(\varepsilon; E_1, \ldots, E_n)\varphi_i(x_i^*(\varepsilon; E_1, \ldots, E_n)) - E_i x_i^*(\varepsilon; E_1, \ldots, E_n) \\ + \varepsilon \sum_{j=1}^{n} \gamma_{ij} x_i^*(\varepsilon; E_1, \ldots, E_n) = 0 \quad i = 1, \ldots, n. \end{aligned} \tag{4.3}$$

The yield Y_i^* is given by

$$Y_i^*(\varepsilon;E_1,\dots,E_n) = E_i x_i^*(\varepsilon;E_1,\dots,E_n) = x_i^*(\varepsilon;E_1,\dots,E_n)\varphi_i(x_i^*(\varepsilon;E_1,\dots,E_n)) + \varepsilon\sum_{j=1}^{n}\gamma_{ij}x_i^*(\varepsilon;E_1,\dots,E_n) \quad i=1,\dots,n.$$

The sum of Y_i^* for $i=1,\dots,n$ gives the total Yield Y_T^* of n connected patches:

$$Y_T^*(\varepsilon;E_1,\dots,E_n) = \sum_{i=1}^{n} x_i^*(\varepsilon;E_1,\dots,E_n)\varphi_i(x_i^*(\varepsilon;E_1,\dots,E_n)).$$

Hence,

$$Y_{MSY,T}^*(\varepsilon) = \max_{(E_1,\dots,E_n)}\sum_{i=1}^{n} x_i^*(\varepsilon;E_1,\dots,E_n)\varphi_i(x_i^*(\varepsilon;E_1,\dots,E_n)). \tag{4.4}$$

For $\varepsilon = 0$, the sum of MSY of each isolated patches take the following form:

$$\begin{aligned} Y_{MSY,T}^*(0) &= \max_{(E_1,\dots,E_n)}\sum_{i=1}^{n} x_i^*(0;E_i)\varphi_i(x_i^*(0;E_i)) \\ &= \sum_{i=1}^{n}\max_{0\le E_i\le\varphi_i(0)} x_i^*(0;E_i)\varphi_i(x_i^*(0;E_i)) \\ &= \sum_{i=1}^{n}\max_{0\le x_i\le K_i} x_i\varphi_i(x_i). \end{aligned}$$

4.2. **Comparison of MSY catches between connected fishing patches via migration and isolated fishing patches.** Now, we are going to compare at MSY the total yield for the system (4.1), $Y_{MSY,T}^*(\varepsilon)$, given by the formula (4.4), with the sum of yields for n isolated patches, $Y_{MSY,T}^*(0)$, as the migration rate ε varies from 0 to ∞.

Thus, we generalize and extend the results of Auger et al. [4] for the two-patch model with harvesting to the multi-patch model with harvesting (4.1). We have the following result:

Theorem 4.1. *Consider the MSY (4.4) of the total Yield, then, for all $\varepsilon \ge 0$, we have:*

$$Y_{MSY,T}^*(\varepsilon) \le Y_{MSY,T}^*(0).$$

Proof. We have for all $\varepsilon \ge 0$:

$$\begin{aligned} Y_{MSY,T}^*(\varepsilon) &= \max_{(E_1,\dots,E_n)}\sum_{i=1}^{n} x_i^*(\varepsilon;E_1,\dots,E_n)\varphi_i(x_i^*(\varepsilon;E_1,\dots,E_n)), \\ &\le \max_{(E_1,\dots,E_n)}\sum_{i=1}^{n}\max_{x_i} x_i\varphi_i(x_i), \\ &\le Y_{MSY,T}^*(0). \end{aligned}$$

□

As a first corollary of the previous Theorem, we have:

Corollary 1. *Assume that: $\varphi_i(x_i) = r_i\left(1-\dfrac{x_i}{K_i}\right)$ for all i. Consider the MSY (4.4) of the total Yield, then, for all $\varepsilon \ge 0$, we have:*

$$Y_{MSY,T}^*(\varepsilon) \le Y_{MSY,T}^*(0) = \sum_{i=1}^{n}\frac{1}{4}r_iK_i.$$

Proof. The function φ_i satisfies to hypothesis H2. The derivative of $x_i^*\varphi_i(x_i^*)$ with respect to x_i^* gives:

$$\frac{d(x_i^*\varphi_i)}{dx_i^*}(x_i^*) = -r_i\left[-1+2\left(\frac{x_i^*}{K_i}\right)\right].$$

Therefore, $\frac{d(x_i^*\varphi_i)}{dx_i^*}(x_i^*) = 0$ if and only if $x_i^* = \frac{K_i}{2}$. In that case, the maximum of $x_i^*\varphi_i$ is equal to $1/4r_iK_i$. Hence, the completes proof of corollary. □

As a second corollary of the previous Theorem, we have:

Corollary 2. *Assume that:* $\varphi_i(x_i) = r_i\left[1-\left(\frac{x_i}{K_i}\right)^{\mu_i}\right]$ *for all i. Consider the MSY (4.4) of the total Yield, then, for all* $\varepsilon \geq 0$ *and for all* $\mu > 0$*, we have:*

$$Y^*_{MSY,T}(\varepsilon) \leq Y^*_{MSY,T}(0) = \sum_{i=1}^{n} \mu_i \left(\frac{1}{\mu_i+1}\right)^{\mu_i^{-1}+1} r_iK_i.$$

Proof. The function φ_i satisfies to hypothesis H2. The derivative of $x_i^*\varphi_i$ with respect to x_i^* gives:

$$\frac{d(x_i^*\varphi_i)}{dx_i^*}(x_i^*) = -r_i\left[-1+\left(\frac{x_i^*}{K_i}\right)^{\mu_i}+\left(\frac{x_i^*}{K_i}\right)^{\mu_i}\mu_i\right].$$

Therefore, $\frac{d(x_i^*\varphi_i)}{dx_i^*}(x_i^*) = 0$ if and only if $x_i^* = \frac{1}{(\mu_i+1)^{\frac{1}{\mu_i}}}K_i$. In that case, the maximum of $x_i^*\varphi_i$ is equal to $\frac{\mu_i}{\mu_i+1}\left(\frac{1}{\mu_i+1}\right)^{\mu_i^{-1}} r_iK_i$. Hence, the completes proof of corollary. □

As a third corollary of the previous Theorem, we have:

Corollary 3. *Assume that:* $\varphi_i(x_i) = r_i\ln\left(\frac{K_i}{x_i}\right)$ *for all i. Consider the MSY (4.4) of the total Yield, then, for all* $\varepsilon \geq 0$*, we have:*

$$Y^*_{MSY,T}(\varepsilon) \leq Y^*_{MSY,T}(0) = \sum_{i=1}^{n} \frac{1}{e} r_iK_i.$$

Proof. The function φ_i satisfies to hypothesis H2. The derivative of $x_i^*\varphi_i$ with respect to x_i^* gives:

$$\frac{d(x_i^*\varphi_i)}{dx_i^*}(x_i^*) = r_i\ln\left(\frac{K_i}{x_i^*}\right) - r_i$$

Therefore, $\frac{d(x_i^*\varphi_i)}{dx_i^*}(x_i^*) = 0$ if $x_i^* = K_i/e$. In that case, the maximum of $x_i^*\varphi_i$ is equal to $\frac{1}{e}r_iK_i$. Hence, the completes proof of corollary. □

4.3. **Variation of the total yield at MSY as function of migration.** The following theorem establishes a fundamental quantitative relationship between habitat connectivity and sustainable fishery productivity in multi-patch systems. It reveals a universal ecological constraint: in any network of interconnected habitats where populations follow realistic growth dynamics, intensification of migratory exchanges necessarily reduces the maximum sustainable yield (MSY) of the entire system. Mathematically, we have the following result:

Theorem 4.2. *Assume that:* $\varphi_i(x_i) + x_i\varphi_i'(x_i) < 0$ *for all i. Consider the multi-patch system (4.1) under assumptions (H1)-(H4), then, the total maximum sustainable yield* $Y^*_{MSY,T}(\varepsilon)$ *is a decreasing function of the migration rate* ε*, i.e.,*

$$\frac{dY^*_{MSY,T}}{d\varepsilon}(\varepsilon) \leq 0 \quad \text{for all } \varepsilon \geq 0.$$

Proof. At equilibrium ($dx_i/dt = 0$):

$$x_i^* \varphi_i(x_i^*) - E_i x_i^* + \varepsilon \sum_{j=1}^{n} \gamma_{ij} h_j(x_j^*) = 0 \quad (1) \tag{4.5}$$

The total yield is:

$$Y_T^*(\varepsilon) = \sum_{i=1}^{n} E_i x_i^*(\varepsilon) \tag{4.6}$$

Differentiate (4.5) with respect to ε:

$$\left[\varphi_i(x_i^*) + x_i^* \varphi_i'(x_i^*) - E_i\right] \frac{dx_i^*}{d\varepsilon} + \sum_{j=1}^{n} \gamma_{ij} h_j(x_j^*) + \varepsilon \sum_{j=1}^{n} \gamma_{ij} h_j'(x_j^*) \frac{dx_j^*}{d\varepsilon} = 0 \tag{4.7}$$

Denote $\varphi_i(x_i^*) + x_i^* \varphi_i'(x_i^*) := A_i(x_i^*)$. Let $D_i := A_i(x_i^*) - E_i$. The matrix form is:

$$\mathbf{D} \frac{dx^*}{d\varepsilon} + \Gamma h(x^*) + \varepsilon \Gamma \mathbf{H} \frac{dx^*}{d\varepsilon} = 0 \tag{4.8}$$

where: $x^* = (x_1^*, \ldots, x_n^*), \mathbf{D} = \operatorname{diag}(D_1, \ldots, D_n), h(x_1{}^*) = (h_1(x_n{}^*), \ldots, h_n(x^*))^T$ and $\mathbf{H} = \operatorname{diag}(h_1'(x_1^*), \ldots, h_n'(x_n^*))$. The previous equation implies that:

$$[\mathbf{D} + \varepsilon \Gamma \mathbf{H}] \frac{dx^*}{d\varepsilon} = -\Gamma h(x^*) \tag{4.9}$$

Under assumptions (H1)-(H4), the matrix $\mathbf{M} := \mathbf{D} + \varepsilon \Gamma \mathbf{H}$ is invertible for $\varepsilon \geq 0$, Indeed, From the assumption $\varphi_i + x_i \varphi_i' < 0$ and harvesting $E_i \geq 0$, we have:

$$D_i = \varphi_i(x_i^*) + x_i^* \varphi_i'(x_i^*) - E_i < 0 \quad \text{for all } i.$$

For $\varepsilon > 0$, consider the row sums of $\mathbf{M}$:

$$|M_{ii}| - \sum_{j \neq i} |M_{ij}| = |D_i + \varepsilon \Gamma_{ii} h_i'(x_i^*)| - \varepsilon \sum_{j \neq i} |\Gamma_{ij} h_j'(x_j^*)|$$

Since $\Gamma_{ii} = -\sum_{j \neq i} \gamma_{ji} < 0$ and $\Gamma_{ij} = \gamma_{ij} \geq 0$ ($i \neq j$), and $h_j' > 0$ (from H3):

$$|M_{ii}| - \sum_{j \neq i} |M_{ij}| = -D_i - \varepsilon \Gamma_{ii} h_i'(x_i^*) - \varepsilon \sum_{j \neq i} \Gamma_{ij} h_j'(x_j^*) = -D_i + \varepsilon \left(\sum_{j \neq i} \gamma_{ji} h_i'(x_i^*) - \sum_{j \neq i} \gamma_{ij} h_j'(x_j^*) \right)$$

From (H4), Γ is irreducible. By the Levy-Desplanques theorem, a strictly diagonally dominant matrix with non-positive diagonal entries and non-negative off-diagonal entries is non-singular. Here: Diagonal entries $M_{ii} = D_i + \varepsilon \Gamma_{ii} h_i'(x_i^*) < 0$ and Off-diagonal entries $M_{ij} = \varepsilon \Gamma_{ij} h_j'(x_j^*) \geq 0$ for $i \neq j$. The matrix $\mathbf{M}$ can be written as:

$$\mathbf{M} = \mathbf{D} + \varepsilon \Gamma \mathbf{H} = \mathbf{D} - \varepsilon \tilde{\Gamma}$$

where $\tilde{\Gamma}$ is a Metzler matrix (non-negative off-diagonal).Since $\mathbf{D} < 0$ (negative definite diagonal) and $\tilde{\Gamma} \geq 0$, the eigenvalues of $\mathbf{M}$ satisfy:

$$\operatorname{Re}(\lambda(\mathbf{M})) \leq \max_i D_i < 0$$

Thus, $\mathbf{M}$ cannot have a zero eigenvalue. Therefore, $\mathbf{D} + \varepsilon \Gamma \mathbf{H}$ is invertible for all $\varepsilon \geq 0$. Hence,

$$\frac{dx^*}{d\varepsilon} = -[\mathbf{D} + \varepsilon \Gamma \mathbf{H}]^{-1} \Gamma h(x^*) \tag{4.10}$$

Yield Derivative is given by:

$$\frac{dY_T^*}{d\varepsilon} = E^\top \frac{dx^*}{d\varepsilon} = -E^\top [\mathbf{D} + \varepsilon \Gamma \mathbf{H}]^{-1} \Gamma h(x^*) \tag{4.11}$$

We have, For $\varepsilon \geq 0$: Γ is Metzler with negative diagonal (H4), the vector $h(x^*) \geq 0$ component-wise (H3) and $[\mathbf{D}+\varepsilon\Gamma\mathbf{H}]^{-1}$ is non-positive. Thus:

$$\frac{dY_T^*}{d\varepsilon} = -\underbrace{E^\top}_{\geq 0}\underbrace{[\mathbf{D}+\varepsilon\Gamma\mathbf{H}]^{-1}}_{\leq 0}\underbrace{\Gamma}_{\leq 0}\underbrace{h(x^*)}_{\geq 0} \leq 0 \tag{4.12}$$

□

Example 4. *For identical patches with symmetric migration, the equilibrium equations are:*

$$\begin{cases} rx_1^*\left(1-\frac{x_1^*}{K}\right) - Ex_1^* + \varepsilon\gamma(x_2^*-x_1^*) &= 0 \\ rx_2^*\left(1-\frac{x_2^*}{K}\right) - Ex_2^* + \varepsilon\gamma(x_1^*-x_2^*) &= 0 \end{cases} \tag{4.13}$$

Rewrite (4.13) as:

$$\begin{pmatrix} r(1-\frac{2x_1^*}{K}) - E - \varepsilon\gamma & \varepsilon\gamma \\ \varepsilon\gamma & r(1-\frac{2x_2^*}{K}) - E - \varepsilon\gamma \end{pmatrix} \begin{pmatrix} dx_1^*/d\varepsilon \\ dx_2^*/d\varepsilon \end{pmatrix} = -\gamma \begin{pmatrix} x_2^*-x_1^* \\ x_1^*-x_2^* \end{pmatrix} \tag{4.14}$$

The total yield is $Y_T^* = E(x_1^*+x_2^*)$. Its derivative:

$$\frac{dY_T^*}{d\varepsilon} = E\left(\frac{dx_1^*}{d\varepsilon}+\frac{dx_2^*}{d\varepsilon}\right) = -E\gamma\begin{pmatrix}1 & 1\end{pmatrix}\mathbf{J}^{-1}\begin{pmatrix} x_2^*-x_1^* \\ x_1^*-x_2^* \end{pmatrix} \tag{4.15}$$

where $\mathbf{J}$ is the Jacobian matrix evaluated at equilibrium.
At MSY, $E = r/2$ and $x_1^* = x_2^* = K/2$. The Jacobian becomes:

$$\mathbf{J} = \begin{pmatrix} -r-\varepsilon\gamma & \varepsilon\gamma \\ \varepsilon\gamma & -r-\varepsilon\gamma \end{pmatrix} \tag{4.16}$$

with inverse:

$$\mathbf{J}^{-1} = \frac{1}{(r+\varepsilon\gamma)^2-(\varepsilon\gamma)^2}\begin{pmatrix} -r-\varepsilon\gamma & -\varepsilon\gamma \\ -\varepsilon\gamma & -r-\varepsilon\gamma \end{pmatrix} \tag{4.17}$$

Substituting into (4.15):

$$\frac{dY_T^*}{d\varepsilon} = -\frac{r}{2}\gamma\begin{pmatrix}1 & 1\end{pmatrix}\frac{1}{r(r+2\varepsilon\gamma)}\begin{pmatrix} -r-\varepsilon\gamma & -\varepsilon\gamma \\ -\varepsilon\gamma & -r-\varepsilon\gamma \end{pmatrix}\begin{pmatrix}0\\0\end{pmatrix} = -\frac{r^2K\gamma}{2(r+2\varepsilon\gamma)^2} \tag{4.18}$$

Alternatively, starting from the symmetric solution:

$$x^* = \frac{K(r-E)}{r+2\varepsilon\gamma} \tag{4.19}$$

Total yield at MSY ($E = r/2$):

$$Y_{MSY}^* = 2\cdot\frac{r}{2}\cdot\frac{K(r-r/2)}{r+2\varepsilon\gamma} = \frac{r^2K}{2(r+2\varepsilon\gamma)} \tag{4.20}$$

Differentiating:

$$\frac{dY_{MSY}^*}{d\varepsilon} = -\frac{r^2K\cdot 2\gamma}{2(r+2\varepsilon\gamma)^2} = -\frac{r^2K\gamma}{(r+2\varepsilon\gamma)^2} \tag{4.21}$$

5. **Numerical simulations.** In this section, we will conduct some numerical simulations to further investigate the effect of different parameters of the model and interconnections on the Maximum Sustainable Yield in a heterogeneous environment and demonstrate our theoretical findings of TheoremS 4.1 and 4.2. Note that, the parameter values used below are for illustrative purposes only and are not intended to be biologically realistic.

5.1. **Illustration the result of Theorem 4.1.**

Example 5. *We consider the system of two patch with harvesting, i.e.* (4.1) *and we assume that the first patch follows a logistic law, while the second patch follows a Richards law. The model read as follow:*

$$\begin{cases} \dfrac{dx_1}{dt} = 2x_1(1-x_1) - E_1x_1 + \varepsilon(x_2 - x_1), \\ \dfrac{dx_2}{dt} = 3x_2\left(1 - \left[\dfrac{x_2}{2}\right]^2\right) - E_2x_2 + \varepsilon(x_1 - x_2). \end{cases} \tag{5.1}$$

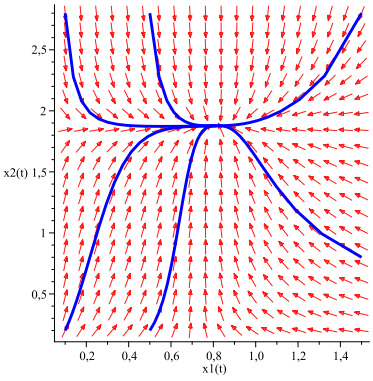


FIGURE 4. Trajectories of the Coupled System (5.1) with $E_1 = 0.5, E_2 = 0.3, \varepsilon = 0.1$

The sum of MSY of each isolated patches ($\varepsilon = 0$) is given by

$$Y^*_{MSY,T}(0) = \mu_1\left(\frac{1}{\mu_1+1}\right)^{\mu_1^{-1}+1} r_1K_1 + \mu_2\left(\frac{1}{\mu_2+1}\right)^{\mu_2^{-1}+1} r_2K_2 \simeq 2.809401076. \tag{5.2}$$

Example 6. *We consider the system of two patch with harvesting, i.e.* (4.1) *and we assume that the both patches follows a Gompertz law. The model read as follow:*

$$\begin{cases} \dfrac{dx_1}{dt} = 3x_1\ln\left(\dfrac{1}{x_1}\right) - E_1x_1 + \varepsilon(2x_2 - x_1), \\ \dfrac{dx_2}{dt} = 2x_2\ln\left(\dfrac{4}{x_2}\right) - E_2x_2 + \varepsilon(x_1 - 2x_2). \end{cases} \tag{5.3}$$

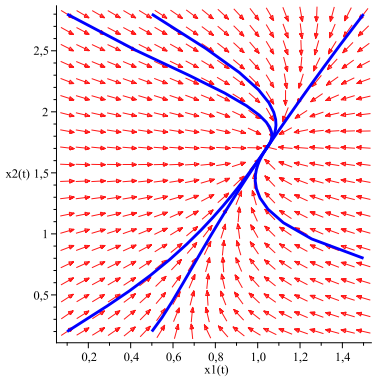


FIGURE 5. Trajectories of the Coupled System (5.3) with $E_1 = 1, E_2 = 1, \varepsilon = 0.5$

The sum of MSY of each isolated patches ($\varepsilon = 0$) is given by

$$Y^*_{MSY,T}(0) = 1/e(r_1K_1 + r_2K_2) \simeq 4.046673854. \tag{5.4}$$

We propose here to plot the total yield $Y^*_T(\varepsilon, E_1, E_2) = (Y^*_1 + Y^*_2)(\varepsilon, E_1, E_2)$ with respect to the fishing efforts E_1 and E_2 and also these projections in the plan $E_1 = 0$ and $E_2 = 0$, for $\varepsilon = 0$ and for $\varepsilon \to \infty$.

In the table 1, we compute $Y^*_{MSY,T}(\varepsilon), (\triangle Y^*_{MSY,T})(\varepsilon)$ and $\%\triangle Y^*_{MSY,T}$. The Yield excess $\triangle Y^*_{MSY,T}$ is given by the following formula:

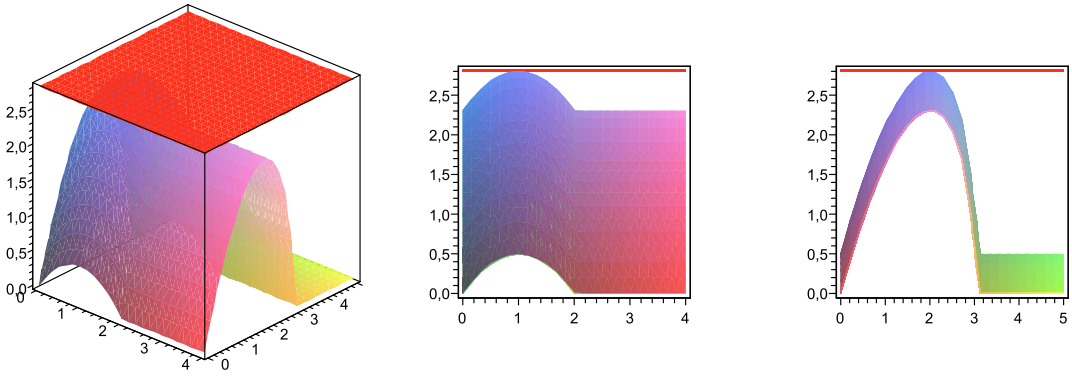
$$(\triangle Y^*_{MSY,T})(\varepsilon) = Y^*_{MSY,T}(\varepsilon) - Y^*_{MSY,T}(0),$$

and the percentage of yield excess is define as:

$$(\%\triangle Y^*_{MSY,T})(\varepsilon) = 100\frac{(\triangle Y^*_{MSY,T})(\varepsilon)}{Y^*_{MSY,T}(\varepsilon)}.$$

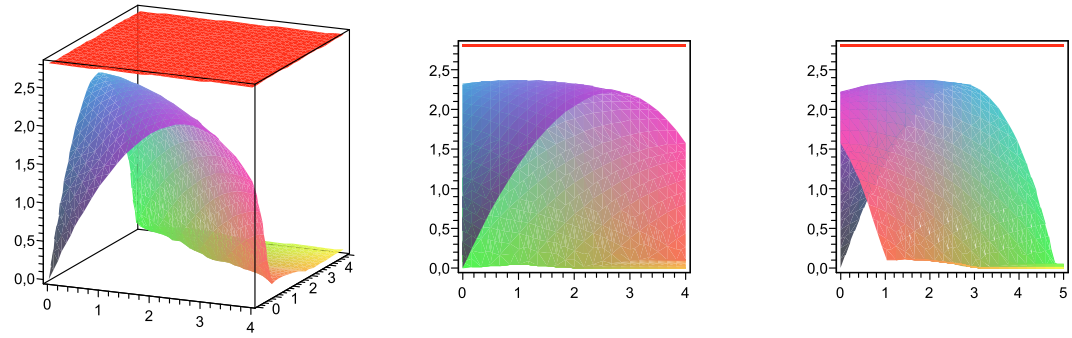
TABLE 1. Values of $Y_{MSY,T}$ and $\triangle Y_{MSY,T}$ obtained for the models (5.1) and (5.3) and for migration rate $\varepsilon = 0$ and ε close to ∞.

Figures	ε	$Y^*_{MSY,T}(\varepsilon)$	$(\triangle Y^*_{MSY,T})(\varepsilon)$	$\%\triangle Y^*_{MSY,T}$
Fig. 6	0	2.80	-0.00	00.00%
Fig. 7	∞	2.30	-0.50	21.73%
Fig. 8	0	4.04	-0.00	00.00%
Fig. 9	∞	2.68	-1.36	50.74%



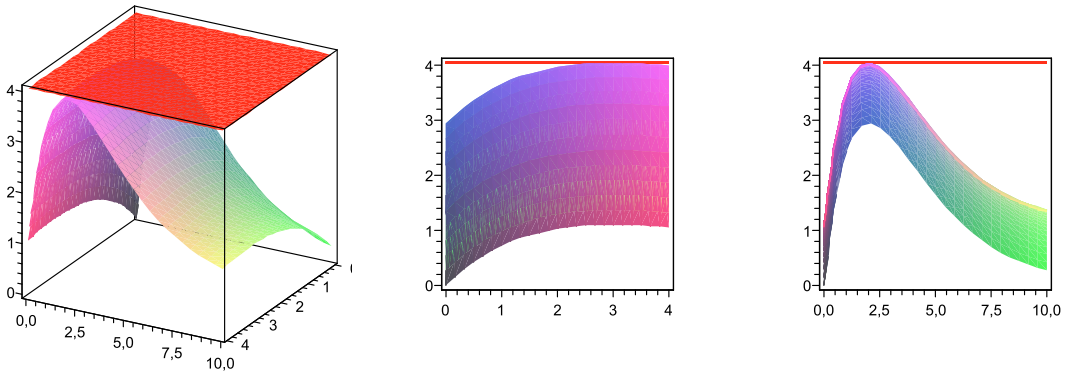
(a) (b) (c)

FIGURE 6. Case a: The total yield $Y_T^*(0,E_1,E_2) = (Y_1^* + Y_2^*)(0,E_1,E_2)$ with respect to the fishing effort $E_1 \in [0,4]$ and $E_2 \in [0,5]$ which is shown in blue, and the total yield $Y_T^*(0,E_1,E_2) = 2.80$ is shown in red for the model 5.1 and the migration rate ε equal to 0. Case b (resp. c): the projection of the total yields $Y_T^*(0,E_1,E_2)$ and $Y_T^*(0,E_1,E_2) \simeq 2.80$ in



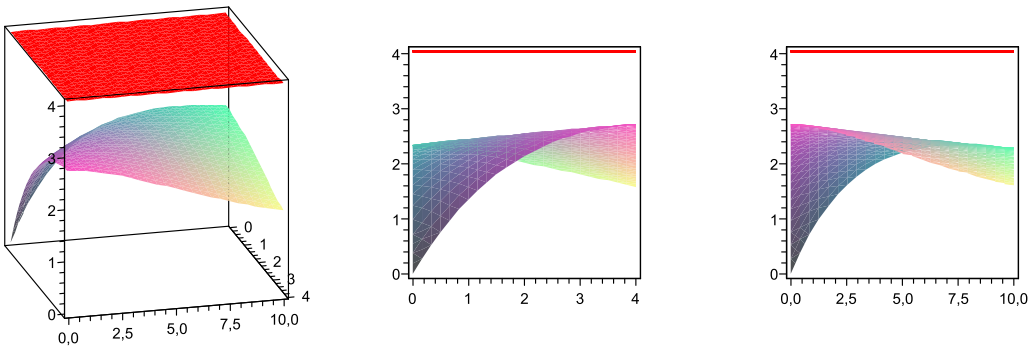
(a) (b) (c)

FIGURE 7. Case a: The total yield $Y_T^*(\infty,E_1,E_2) = (Y_1^* + Y_2^*)(\infty,E_1,E_2)$ with respect to the fishing effort $E_1 \in [0,4]$ and $E_2 \in [0,5]$ which is shown in blue, and the total yield $Y_T^*(0,E_1,E_2) = 2.80$ is shown in red for the model 5.1 and the migration rate $\varepsilon \to \infty$. Case b (resp. c): the projection of the total yields $Y_T^*(\infty,E_1,E_2)$ and $Y_T^*(0,E_1,E_2) \simeq 2.80$ in the plan $E_2 = 0$ (resp. $E_1 = 0$).



(a) (b) (c)

FIGURE 8. Case a: The total yield $Y_T^*(0,E_1,E_2) = (Y_1^* + Y_2^*)(0,E_1,E_2)$ with respect to the fishing effort $E_1 \in [0,4]$ and $E_2 \in [0,10]$ which is shown in blue, and the total yield $Y_T^*(0,E_1,E_2) = 4.04$ is shown in red for the model 5.3 and the migration rate ε equal to 0. Case b (resp. c): the projection of the total yields $Y_T^*(0,E_1,E_2)$ and $Y_T^*(0,E_1,E_2) \simeq 4.04$ in the plan $E_2 = 0$ (resp. $E_1 = 0$).



(a) (b) (c)

FIGURE 9. Case a: The total yield $Y_T^*(\infty,E_1,E_2) = (Y_1^* + Y_2^*)(\infty,E_1,E_2)$ with respect to the fishing effort $E_1 \in [0,4]$ and $E_2 \in [0,10]$ which is shown in blue, and the total yield $Y_T^*(0,E_1,E_2) = 4.04$ is shown in red for the model 5.3 and the migration rate $\varepsilon \to \infty$. Case b (resp. c): the projection of the total yields $Y_T^*(0,E_1,E_2)$ and $Y_T^*(0,E_1,E_2) \simeq 4.04$ in the plan $E_2 = 0$ (resp. $E_1 = 0$).

5.2. **Illustration the result of Theorem 4.2.** The four curves in Figures 12 and 15 present a comparative analysis of how migration rates (ε) affect the total yield at MSY ($Y_{MSY,T}^*$) across different population models. Each figure illustrates distinct biological growth dynamics: (1) Logistic-Richards with $Y_{MSY,T}^*(0) = 2.809$, (2) Gompertz-Gompertz with $Y_{MSY,T}^*(0) = 4.047$, (3) Logistic-Logistic with $Y_{MSY,T}^*(0) = 3.500$, and (4) Richards-Richards with $Y_{MSY,T}^*(0) = 3.200$.

All models demonstrate an exponential decay in total yield at MSY as migration rate ε increases, with two key observations:

First, the Gompertz model shows the steepest decline due to its logarithmic growth constraint, with total yields at MSY dropping by approximately 34% at $\varepsilon = 5$.

Second, models with asymmetric parameters (Richards) exhibit a slower decay (only an 18% reduction at $\varepsilon = 5$), suggesting greater structural resilience to migration effects.

This analysis highlights a fundamental trade-off in resource management: while migration enhances ecological connectivity, it systematically reduces short-term profitability, with the severity depending on the population's growth characteristics. The results suggest that optimal fishery management should account for both species-specific growth dynamics and patch connectivity levels when setting harvesting policies. In particular:

- Fisheries dominated by Gompertz-type growth require more conservative management at high migration rates.
- Richards-type systems may tolerate higher connectivity while maintaining yields.

6. **Conclusion and Perspectives.** In this work, we investigated the influence of generalized growth functions on the determination of the Maximum Sustainable Yield (MSY) in both single-species and spatially structured multi-patch fishery models. Starting with a general formulation of population growth, we analyzed how different functional forms specifically the logistic, Richards, and Gompertz models affect the equilibrium biomass under harvesting and derived explicit expressions for MSY in each case. These results reveal that the intrinsic shape of the growth function directly influences both the optimal biomass level and the corresponding harvesting effort, thus affecting management recommendations. Notably, the Richards model with its adjustable shape parameter offers a flexible framework that encompasses the logistic model as a special case and allows higher yields under certain conditions.

In the multi-patch setting, we extended the analysis to systems with spatial dispersal between patches and demonstrated, both analytically and numerically, that the total MSY of a connected system is always less than or equal to the sum of MSYs obtained when patches are managed in isolation. This result holds under general biological assumptions and is shown to be robust across different growth models and migration patterns. Moreover, we proved that the total yield at MSY decreases monotonically with increasing migration rate, highlighting a counterintuitive trade-off: while dispersal may enhance population persistence, it simultaneously reduces the maximum yield that can be sustainably harvested from the entire system. These findings provide a rigorous theoretical foundation for understanding how spatial connectivity and intrinsic growth dynamics interact to shape harvesting potential in ecological systems.

To further improve the ecological relevance and practical utility of the proposed modeling approach, future work could explore several valuable extensions. A key direction is the incorporation of predator–prey dynamics, especially in situations where the predator is also subject to harvesting. This would provide a richer representation of trophic interactions and their implications for the sustainable management of ecosystems. Additionally, introducing stochastic components—such as environmental fluctuations or demographic randomness—would allow for the analysis of MSY under uncertain conditions, thereby enhancing the robustness and reliability of management recommendations.

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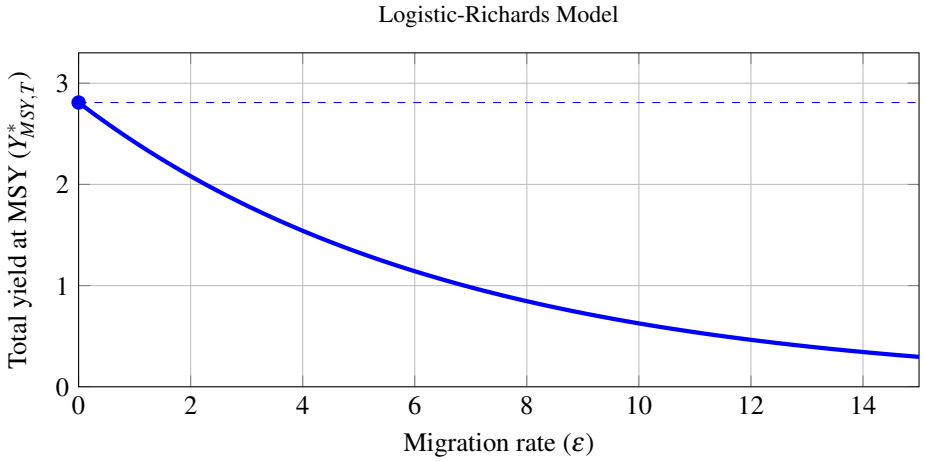

FIGURE 10. Parameters: $r_1 = 2$, $K_1 = 1$, $\mu = 2$
Initial profit: $Y^*_{MSY,T}(0) = 2.809$

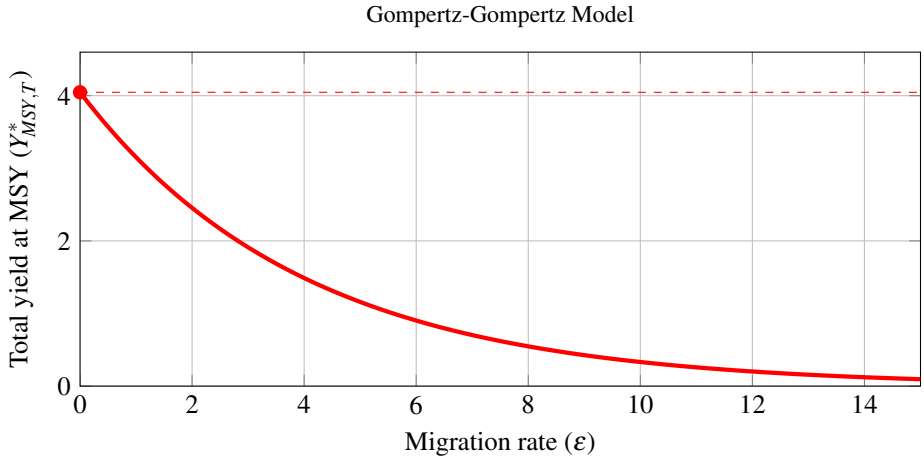

FIGURE 11. Parameters: $r_1 = 3$, $K_1 = 1$, $r_2 = 2$, $K_2 = 4$
Initial profit: $Y^*_{MSY,T}(0) = 4.047$

FIGURE 12. Impact of migration rate on total yield at MSY, $Y^*_{MSY,T}$, for different population models for two patches case.

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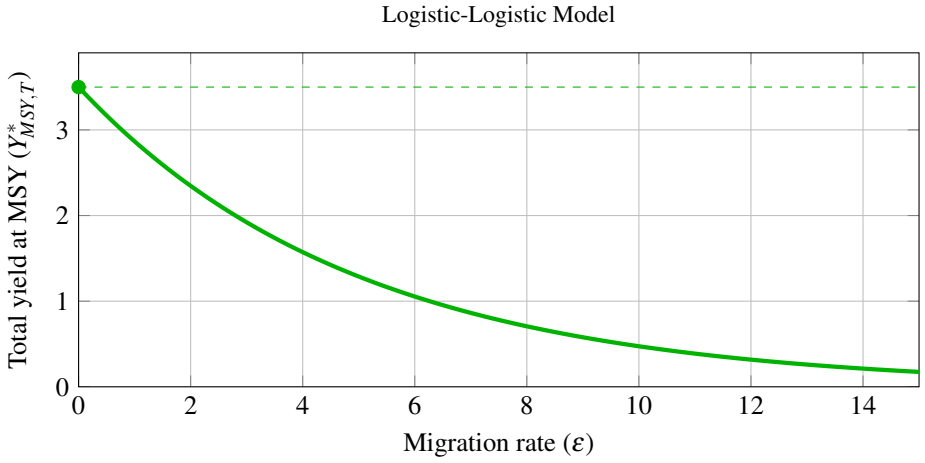

FIGURE 13. Parameters: $r_1 = 2.5$, $K_1 = 1.4$, $r_2 = 2$, $K_2 = 1.8$ Initial profit: $Y^*_{MSY,T}(0) = 3.500$.

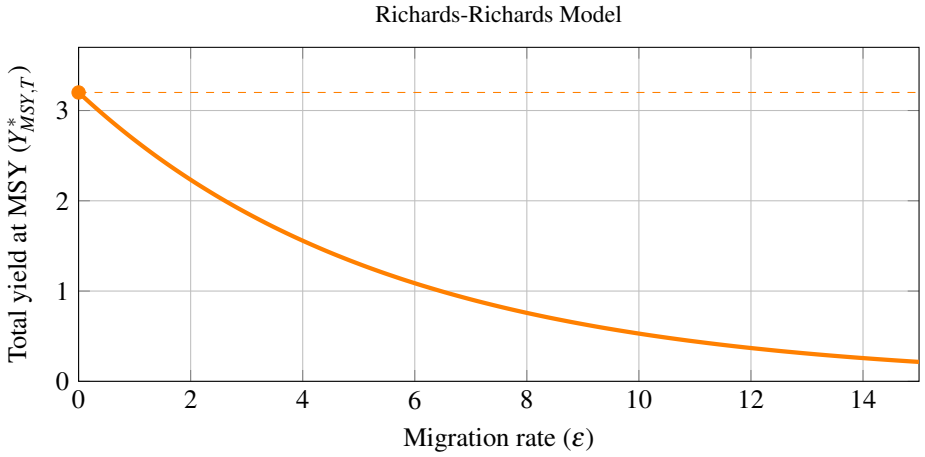

FIGURE 14. Parameters: $r_1 = 3$, $K_1 = 1.2$, $\mu_1 = 1.5$ $r_2 = 2.5$, $K_2 = 1.5$, $\mu_2 = 2$ Initial profit: $Y^*_{MSY,T}(0) = 3.200$

FIGURE 15. Impact of migration rate on total yield at MSY, $Y^*_{MSY,T}$, for different population models for two patches case.

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