Math. Model. Nat. Phenom. 18 (2023) 4
https://doi.org/10.1051/mmnp/2023004

Mathematical Modelling of Natural Phenomena
www.mmnp-journal.org

THE EFFECT OF CONNECTING SITES IN THE ENVIRONMENT OF A HARVESTED POPULATION

Rafael Bravo de la Parra[1,*], Jean-Christophe Poggiale[2] and Pierre Auger[3]

Abstract. This work presents a model of a harvested population in a multisite environment. Locally it has the shape of the Gordon-Schaefer model. This model gives rise, placing us in the case of a fishery, to an equilibrium of the stock and the fishing effort and, therefore, of the yield that is obtained per unit of time. Considering that the management of the fishery can act on the fishing costs, the yield is optimized as a function of the cost. The objective of the work is to compare the maximum obtained yield in two extreme cases: unconnected sites and connected sites with rapid movements of both the stock and the fishing effort. The analysis of the model, first in an environment with two sites and later with any number of them, makes it possible to establish the conditions for one of the two cases to be more favorable from the point of view of the yield. In this way, it is proposed towards which of the two compared cases management should be directed.

Mathematics Subject Classification. 34A34, 92D25.

Received September 1, 2022. Accepted January 18, 2023.

1. Introduction

Multisite fisheries consist of a network of discrete fishing sites connected to each other by fish movements. Some sites can be created by man as areas where fishing is totally prohibited such as marine protected areas (MPA), [16], or partially prohibited, especially at certain periods of the year. Other fishing areas are intentionally created as fish aggregating devices (FADs) because they attract fish that can be caught there more easily, [13] and [10]. The various fishing zones generally correspond to heterogeneous sites, in particular with regard to the environmental characteristics, such as the surface of the zone, the depth, the presence of a shelter zone, the underwater vegetation or even the resources available for the growth of the various species of commercial fish. All these local characteristics of the fishing sites affect the growth rate and carrying capacity of the fish species which is usually assumed to grow logistically. Heterogeneity can also result from human intervention, in particular by installing reefs or artificial habitats (AHs). AHs are known to increase the carrying capacity of the site where they are installed [22] and attract fish [7]. In the case of a heterogeneous multisite fishery made up of sites that are more or less rich in the resources available for the fish, it is frequently assumed that the

Keywords and phrases: Multisite fishery, Gordon-Schaefer model, time scales, maximum sustainable yield.

[1] U.D. Matemáticas, Universidad de Alcalá, 28871 Alcalá de Henares, Spain.
[2] CNRS/INSU, Université de Toulon, IRD, Mediterranean Institute of Oceanography (MIO) UM 110, Aix Marseille Université, Campus de Luminy, 13288 Marseille, France.
[3] UMMISCO, Sorbonne Université, Institut de Recherche pour le Développement, IRD, 93143 Bondy, France.

* Corresponding author: rafael.bravo@uah.es

fish are distributed according to the resource available on each site. Fish will be more numerous in resource-rich areas than in poorer areas. For logistic sites, when the fish are distributed among them proportionally to the corresponding carrying capacities, they are said to adopt the Ideal Free Distribution (IFD), [6] and [15].

In the case of a single fishing site, without adding economic assumptions, it is usual to consider the Schaefer model, [9, 23]:

$$N' = rN\Big(1 - \frac{N}{K}\Big) - qEN \tag{1.1}$$

It represents a population of size (stock) $N(t)$ at time t, whose growth is depicted by the logistic model with intrinsic growth rate $r > 0$ and carrying capacity K. The exploitation term, qEN, follows the catch-per-unit-effort hypothesis and, thus, it is proportional to the stock level, with E denoting the constant fishing effort and constant q being the catchability coefficient. If $r - qE > 0$, for any positive initial condition, $N(t)$ tends to an equilibrium $N^* = K(1 - qE/r)$. It is also well known [9] that the yield at equilibrium $Y(E) = qK(1 - qE/r)E$, as function of E, attains its maximum for $E_{MSY} = r/(2q)$. The corresponding yield, called maximum sustainable yield (MSY), is $Y_{MSY} = rK/4$, and the equilibrium stock biomass is $N_{MSY} = K/2$.

In [5] a simple spatialized version of Schaefer's model is studied. Only two sites are considered and the local dynamics is of the form (1.1). Furthermore, the fish stock move between the two sites on a faster time scale than that associated with local dynamics:

$$\begin{aligned} \frac{\mathrm{d}N_1}{\mathrm{d}\tau} &= m_2N_2 - m_1N_1 + \varepsilon\big(r_1N_1(1 - \frac{N_1}{K_1}) - qE_1N_1\big) \\ \frac{\mathrm{d}N_2}{\mathrm{d}\tau} &= m_1N_1 - m_2N_2 + \varepsilon\big(r_2N_2(1 - \frac{N_2}{K_2}) - qE_2N_2\big) \end{aligned} \tag{1.2}$$

For $i = 1, 2$, N_i is the population density on site i. Parameters r_i, K_i, and E_i represent the intrinsic growth rate, the carrying capacity, and the fishing effort, respectively, on site i. The catchability is q. The movement rates for the stock, m_i, are constant and site dependent. Time scales are included in the model by using the fast time variable τ together with the small positive parameter ε that represents their ratio.

As a consequence of the existence of two time scales, the two-dimensional model (1.2) can be analyzed through a one-dimensional Schaefer-type model. The MSY of (1.2) is easily approximated with the help of this one-dimensional model. From it, it is straightforward to compare the MSY for connected and isolated sites. In this latter case the MSY is calculated just by adding the two local MSY. An important result obtained in [5] is that the MSY for a system of two connected fishing sites is always less than or equal to the MSY of the system with isolated sites. Thus, there is no interest in facilitating the connection between the sites because this would not increase the MSY of the system. This is the conclusion when we have not yet brought economic issues into the model.

Fishing boats also travel between the various fishing areas. The fishing boats are evenly distributed among the various fishing areas, avoiding having to meet all at the same time on the same site. The distribution of the boats in the fishing fleet on the different sites has an effect on the overall catch made on the multisite fishery. In a global way, the combined distribution of fish stock and fishing vessels among the various fishing areas has a significant effect on the overall catch of the multisite fishery, [8].

From the shipowner's point of view, it is important to distribute the fishing fleet over the different fishing areas to maximize his benefit which is constituted by the catch multiplied by the price of the resource on the market, which is usually called the landed value. The net income is obtained by subtracting from it the various operating costs of the fishery, such as the price of fuel necessary for the boats, the various taxes to be paid to the government, the wages of the fishermen, the maintenance of the vessels and again the minimum profit desired which corresponds to a threshold below which the shipowner considers that the fishing operation is not sufficiently profitable. The operating costs of the fishery therefore constitute an important parameter and it is legitimate to seek the cost per unit of fishing effort allowing the overall catch of a multisite fishery to be optimized.

To deal with this question it is necessary to introduce the economy in Schaefer's model. A widespread way of doing this is to consider fishing effort as a system variable whose rate of change is proportional to the benefit, *i.e.*, the difference between revenue and cost. An alternative way of introducing the economy is to consider, along with the stock variable, the capital of investment in the activity of fishing, see [19] and the references it includes. We use Gordon's model of an open access fishery together with Schaefer's model to approach the analysis that we propose in this work. We want to study the conditions for a network of discrete fishing sites, connected to each other by fast displacements, to obtain a higher or lower fishing yield than if the sites were isolated.

We highlight the importance of the cost per unit of fishing effort by choosing it as the parameter to calculate the MSY. The Gordon-Schaefer model, if benefit is positive when the stock is at its carrying capacity, has a positive equilibrium to which all positive solutions tend. With the constant values that this equilibrium gives us for the stock and the fishing effort, the yield expression, that depends on all model parameters, is obtained. The maximum of this expression as a function of cost c is what we consider to be the MSY.

We assume that the fishing sites are relatively close to each other allowing fast movements of the stock and the fishing fleet between these various fishing areas. When the sites are close enough, it makes sense to consider that the operating costs are the same in all fishing areas, same wages, taxes, fuel and maintenance costs as well as minimum profit required. The government or the national fisheries management institution has no reason to impose different taxes on fishing sites close to each other.

Starting from the previous hypotheses, in this work, for a multisite fishery, we develop a comparison between the MSY with connected sites and with isolated sites. For it, in Section 2 we recall the basic Gordon-Schaefer model results including the optimization of the sustainable yield in terms of the cost. Section 3 considers a multisite fishery with two fishing sites and compares the MSY in the case where the sites are connected by movements of the stock and the fishing effort to the case where the sites are isolated in the absence of migrations. Section 4 extends the previous results to a multisite fishery with any number of sites. The manuscript ends with a discussion of the results, a conclusion and application perspectives.

2. A single-site harvested population model

As said in the introduction, the influence of economics on harvesting of renewable resources can be described with the help of the Gordon model of an open-access fishery, that is one in which anyone can harvest the resource. In its simplest form it is assumed a constant price p per unit of harvested biomass, so that the total revenue is obtained as $pY(E)$, where $Y(E)$ is the yield resulting from the effort E. The total cost is expressed as cE where c is a constant representing the cost per effort unit. Finally, the effort is considered variable with its rate of change being equal to the benefit $pY(E) - cE$. Equation (1.1) together with the effort equation give the following simple model that it is at the base of all the models that we are presenting.

$$\begin{aligned} \frac{\mathrm{d}N}{\mathrm{d}t} &= rN\big(1-\frac{N}{K}\big) - qEN \\ \frac{\mathrm{d}E}{\mathrm{d}t} &= pqEN - cE \end{aligned} \tag{2.1}$$

We refer to (2.1) as the basic Gordon-Schaefer model. It has the same form as the Lotka-Volterra predator-prey model with prey logistic growth [18]. The asymptotic behaviour of its solutions is simply expressed. If $c < pqK$, *i.e.*, the benefit is positive when the stock is at the carrying capacity, then all positive solutions of the system tend to the so-called bionomic equilibrium:

$$N^* = \frac{c}{pq}, \quad E^* = \frac{r}{q}\left(1 - \frac{c}{pqK}\right), \tag{2.2}$$

with an associated yield

$$Y^* = \frac{rc}{pq}\left(1 - \frac{c}{pqK}\right). \tag{2.3}$$

In the open-access fishery, Gordon-Schaefer model, the fishery effort and the stock tend to reach an equilibrium at the level at which the benefit vanishes [9], as the E equation imposes. This occurs regardless of the initial conditions of both stock and effort.

In the models that we are presenting, we consider the cost per unit of effort as a parameter that the manager can change, by providing the fishers with subventions to decrease it or by setting up some taxes to increase it. We thus look for a maximum sustainable yield considering the yield so far obtained as a function of the cost c.

In model (2.1), the value of c that maximizes the equilibrium yield (2.3) is

$$c_{opt} = \frac{1}{2}pqK, \tag{2.4}$$

obtaining

$$Y_{opt} = \frac{1}{4}rK, \quad \text{with } N_{opt} = \frac{1}{2}K \quad \text{and } E_{opt} = \frac{r}{2q}. \tag{2.5}$$

So, we recuperate the situation of MSY (1.1) of the constant effort case.

Notice that c_{opt} is one half of the maximum cost yielding positive benefit. It leads the stock N_{opt} to one half of the environment carrying capacity K, that is the population size with the largest growth rate. Both, the optimal cost c_{opt} and the stock N_{opt}, as well as the optimal yield Y_{opt} are proportional to K. Nevertheless, the corresponding effort E_{opt} depends on the ratio intrinsic growth rate to catchability and it is independent of K.

3. A two-site harvested population model

We consider a harvested population in a multisite environment. The objective is showing that the maximum sustainable yield can be larger in a heterogeneous environment where stock and effort can move than it would be in the same environment without movements.

We begin by limiting the multisite environment to two sites. We will extend this for an arbitrary number of sites later on. In each site, the stock-effort dynamics is ruled by a local basic Gordon-Schaefer model (2.1). The movements between sites are described by constant rates and in a first approach, are considered fast in comparison to the local dynamics.

Thus, let us consider the following model:

$$\begin{aligned}
\frac{\mathrm{d}N_1}{\mathrm{d}\tau} &= m_2N_2 - m_1N_1 + \varepsilon\big(r_1N_1(1 - \frac{N_1}{K_1}) - qE_1N_1\big) \\
\frac{\mathrm{d}N_2}{\mathrm{d}\tau} &= m_1N_1 - m_2N_2 + \varepsilon\big(r_2N_2(1 - \frac{N_2}{K_2}) - qE_2N_2\big) \\
\frac{\mathrm{d}E_1}{\mathrm{d}\tau} &= \mu_2E_2 - \mu_1E_1 + \varepsilon\big(pqE_1N_1 - cE_1\big) \\
\frac{\mathrm{d}E_2}{\mathrm{d}\tau} &= \mu_1E_1 - \mu_2E_2 + \varepsilon\big(pqE_2N_2 - cE_2\big)
\end{aligned} \tag{3.1}$$

where, for $i = 1, 2$, N_i and E_i are the population density and the fishing effort on site i. Parameters r_i and K_i represent the intrinsic growth rate and the carrying capacity, respectively, on site i. The catchability q, the price per harvest unit p and the cost per unit effort c are assumed equal in both sites. The movement rates for the stock, m_i, and the effort, μ_i, are constant and site dependent. Time scales are included in the model by using the fast time variable τ together with the positive parameter ε that represents their ratio.

We proceed now to compare the maximum sustainable yield in two different cases. In the first one, that we call *connected sites* case, stock and effort movements are allowed so that the dynamics is defined through system (3.1). In the second one, *unconnected sites* case, there is no stock and effort movements and, therefore, the dynamics is represented by the following independent systems, both with the form of (2.1), for $i = 1, 2$:

$$\begin{aligned} \frac{\mathrm{d}N_i}{\mathrm{d}t} &= r_i N_i \big(1 - \frac{N_i}{K_i}\big) - qE_i N_i \\ \frac{\mathrm{d}E_i}{\mathrm{d}t} &= pqE_i N_i - cE_i \end{aligned} \tag{3.2}$$

System (3.1) is not of the form of system (2.1) but it can be reduced to one of this form. The fact that it includes two time scales allows us to apply the reduction method developed in [3, 4]. It consists in a sort of decoupling the fast and the slow parts of the system.

The fast part of the system corresponds to the movements dynamics. Considering the fast part of the stock equations,

$$N_1' = m_2 N_2 - m_1 N_1, \quad N_2' = m_1 N_1 - m_2 N_2,$$

we note that the total stock $N = N_1 + N_2$, $N' = 0$, is kept invariant. This allows us to substitute N_2 by $N - N_1$ in the first equation $N_1' = m_2 N_2 - m_1 N_1$, obtaining $N_1' = -(m_1 + m_2)N_1 + m_2 N$. This last equation is linear and has a single globally asymptotically stable equilibrium $N\, m_2/(m_1 + m_2)$. Thus, we can conclude that any solution of the stock fast system tends to

$$\left(\frac{m_2}{m_1 + m_2} N, \frac{m_1}{m_1 + m_2} N \right).$$

Therefore, the fast movements rapidly tend to distribute the stock between patches according to the following equilibrium proportions:

$$u_1 = \frac{m_2}{m_1 + m_2} \quad \text{and} \quad u_2 = \frac{m_1}{m_1 + m_2}.$$

The same arguments made with the fast part of the effort equations lead us to conclude that the total effort $E = E_1 + E_2$ remains constant and that it quickly tends towards a distribution with the following equilibrium proportions:

$$v_1 = \frac{\mu_2}{\mu_1 + \mu_2} \quad \text{and} \quad v_2 = \frac{\mu_1}{\mu_1 + \mu_2}.$$

If we assume now that the movements have brought stock and effort to their equilibrium proportions, we can write a reduced system for the total stock and effort in terms of the slow time variable $t = \varepsilon\tau$. We add the two stock equations and the two effort equations, and substitute each of the state variables by the corresponding total variable times the associated site proportion, *i.e.*, for $i = 1, 2$, $N_i = Nu_i$ and $E_i = Ev_i$:

$$\begin{aligned} \frac{\mathrm{d}N}{\mathrm{d}t} &= \frac{d(N_1 + N_2)}{\mathrm{d}t} = r_1 N u_1 \Big(1 - \frac{N u_1}{K_1}\Big) - qEv_1 N u_1 + r_2 N u_2 \Big(1 - \frac{N u_2}{K_2}\Big) - qEv_2 N u_2 \\ \frac{\mathrm{d}E}{\mathrm{d}t} &= \frac{d(E_1 + E_2)}{\mathrm{d}t} = pqEv_1 N u_1 - cEv_1 + pqEv_2 N u_2 - cEv_2. \end{aligned}$$

Rearranging terms, it yields the following basic Gordon-Schaefer model:

$$\begin{aligned} \frac{\mathrm{d}N}{\mathrm{d}t} &= \bar{r}N(1-\frac{N}{\bar{K}}) - \bar{q}EN \\ \frac{\mathrm{d}E}{\mathrm{d}t} &= p\bar{q}EN - cE \end{aligned} \tag{3.3}$$

whose parameters, $\bar{r} = r_1u_1 + r_2u_2$, $\bar{K} = \dfrac{(r_1u_1 + r_2u_2)K_1K_2}{r_2u_2^2K_1 + r_1u_1^2K_2}$ and $\bar{q} = q(u_1v_1 + u_2v_2)$, include the local parameters and the equilibrium stock and effort proportions on sites. The so-called aggregated model (3.3) possesses a positive globally asymptotically stable equilibrium provided that $\bar{K} > \dfrac{c}{p\bar{q}}$. It is given, using (2.2), by

$$(\bar{N}, \bar{E}) = \Big(\frac{c}{p\bar{q}}, \frac{\bar{r}}{\bar{q}}(1 - \frac{\bar{N}}{\bar{K}})\Big).$$

The yield at equilibrium is, using (2.3), thus

$$Y = \frac{\bar{r}c}{p\bar{q}}(1 - \frac{c}{p\bar{q}\bar{K}}).$$

Thanks to the aggregated model, all these calculations are very simple and provide us with results concerning the complete model. Figure 1 illustrates that the above mentioned results work perfectly.

To compare the maximum sustainable yield in the connected and unconnected sites cases, we now consider the yield at equilibrium maximized as a function of a single cost. In the first case using system (3.3) and in the second case with the help of systems (3.2).

3.1. Connected sites

The maximum sustainable yield as a function of the cost, in the case with fast movements of the stock and the efforts can be obtained by using (2.4)–(2.5) in system (3.3). For the cost

$$c_{opt} = \frac{1}{2}p\bar{q}\bar{K} = \frac{1}{2}\frac{pq(u_1v_1 + u_2v_2)(r_1u_1 + r_2u_2)K_1K_2}{r_2u_2^2K_1 + r_1u_1^2K_2}$$

the maximum yield is

$$Y_{opt} = \frac{1}{4}\bar{r}\bar{K} = \frac{1}{4}\frac{(r_1u_1 + r_2u_2)^2K_1K_2}{r_2u_2^2K_1 + r_1u_1^2K_2}. \tag{3.4}$$

This expression does not depend on either the price, the catchability or the efforts movements rates. On the other hand, c_{opt} does depend on all of these quantities. The stock and effort at equilibrium are

$$N_{opt} = \frac{1}{2}\bar{K} = \frac{1}{2}\frac{(r_1u_1 + r_2u_2)K_1K_2}{K_1r_2u_2^2 + K_2r_1u_1^2} \quad , \quad E_{opt} = \frac{\bar{r}}{2\bar{q}} = \frac{(r_1u_1 + r_2u_2)}{2q(u_1v_1 + u_2v_2)}.$$

The maximum yield (3.4) is strongly dependent on the equilibrium distribution of the stock to which the movements give rise. Let us show this with the help of a simple case. If we assume two biologically identical

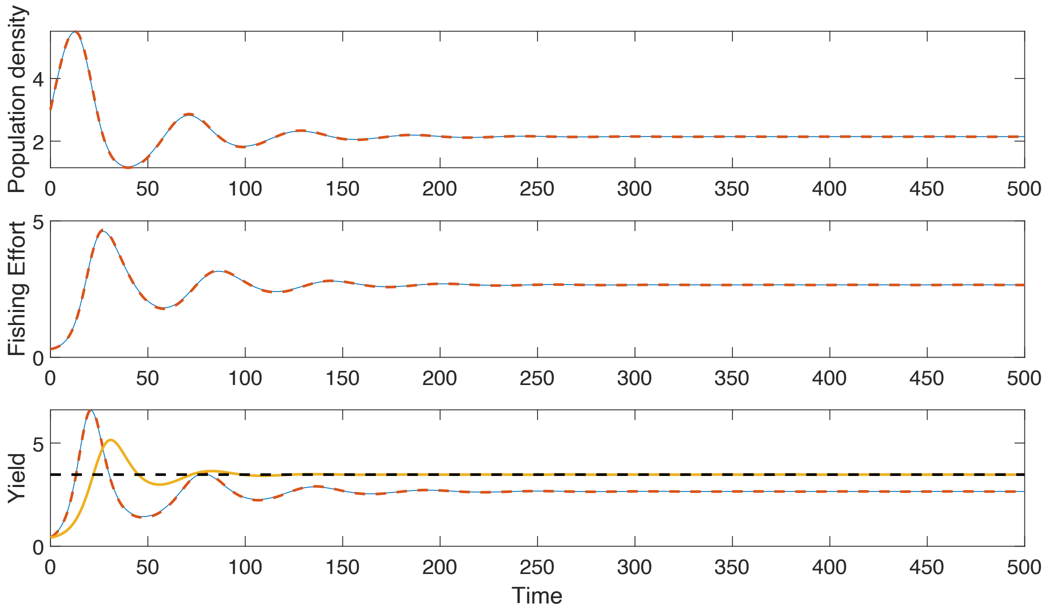


FIGURE 1. Comparison between the complete model (3.1) and the aggregated model (3.3) for the following parameters values: $m_1 = 2$, $m_2 = 1$, $\mu_1 = 2$, $\mu_2 = 3$, $r_1 = 1$, $r_2 = 2$, $K_1 = 5$, $K_2 = 5$, $q = 1$, $p = 1$, and $c = 1$. $\varepsilon = 0.1$ is chosen. Top panel shows the total population density simulated with the complete (blue) and aggregated (dashed red) models. The centre panel shows the effort obtained with the complete (blue) and aggregated (dashed red) models. The bottom panel corresponds to the simulation of the yield. In blue and dashed red respectively are the yields obtained with the complete and aggregated models with the same parameter values as previously. In orange is the yield obtained with the complete model for a cost chosen in a such way that the yield becomes maximal at equilibrium. The dashed black horizontal line is the yield level obtained from the relation $Y_{opt} = rK/4$.

sites, $r_1 = r_2 = r$ and $K_1 = K_2 = K/2$, then we have

$$Y_{opt} = \frac{rK}{4} \cdot \frac{1}{2(u_1^2 + u_2^2)}$$

If the stock is homogeneously distributed, $u_1 = 1/2 = u_2$, then $Y_{opt} = rK/4$, that corresponds to the MSY considering a single stock with biological parameters r and K. Nevertheless, if u_1 approaches 1 and, thus, u_2 approaches 0 (or vice versa), *i.e.*, the stock is mainly established in the first site (or the second one), then Y_{opt} tends to $rK/8$. Uneven stock distribution could almost halve the maximum yield.

Let us see which is the equilibrium stock distribution that maximizes Y_{opt} in a general situation. For this, we consider Y_{opt} as a function of u_1, making $u_2 = 1 - u_1$:

$$Y_{opt}(u_1) = \frac{1}{4} \frac{(r_1 u_1 + r_2(1-u_1))^2 K_1 K_2}{r_2(1-u_1)^2 K_1 + r_1 u_1^2 K_2}.$$

Its derivative can be expressed as

$$Y'_{opt}(u_1) = \frac{r_1 r_2 K_1 K_2 \big(r_1 u_1 + r_2(1-u_1)\big)}{2\big(r_2(1-u_1)^2 K_1 + r_1 u_1^2 K_2\big)^2} \big(K_1 - (K_1 + K_2) u_1\big),$$

and, therefore, its sign just depends on expression $K_1 - (K_1 + K_2)u_1$. The maximum is attained for $u_1 = \dfrac{K_1}{K_1 + K_2}$, that implies $u_2 = \dfrac{K_2}{K_1 + K_2}$. This stock distribution, proportional to the sites carrying capacities, is known in ecological literature as the Ideal Free Distribution (IFD) [15]. The corresponding yield is

$$Y_{opt}\left(\frac{K_1}{K_1 + K_2}\right) = \frac{1}{4}(r_1 K_1 + r_2 K_2),$$

that it is associated to a cost $c_{opt} = \frac{1}{2} pq(K_1 v_1 + K_2 v_2)$ at an equilibrium

$$N_{opt} = \frac{1}{2}(K_1 + K_2) \text{ and } E_{opt} = \frac{1}{2}\frac{r_1 K_1 + r_2 K_2}{q(K_1 v_1 + K_2 v_2)}.$$

The yield $Y_{opt}(u_1)$ grows from $\frac{1}{4} r_2 K_2$, for $u_1 = 0$ (the whole stock living in site 2), to its maximum, at the IFD, and then decreases to $\frac{1}{4} r_1 K_1$, for $u_1 = 0$ (the whole stock living in site 1).

The closer the stock distribution is to the IFD, the larger is the MSY obtained.

In the unconnected case, this question does not apply because, as there are no stock movements, its distribution is constant.

3.2. Unconnected sites

Now, let us assume that there is no movement. The sites are independent of each other from the point of view of stock and effort, though they share the catchability q, the price p, and the cost c.

In this case, the yield of the system is the sum of the yields on each separate site. Using expression (2.3) in both systems (3.2), one gets:

$$Y_S = \frac{r_1 c}{pq}\left(1 - \frac{c}{pqK_1}\right) + \frac{r_2 c}{pq}\left(1 - \frac{c}{pqK_2}\right)$$

As a function of c, Y_S has a maximum for the cost $c_{S,opt} = \dfrac{(r_1 + r_2)pqK_1K_2}{2(r_1K_2 + r_2K_1)}$ equal to

$$Y_{S,opt} = \frac{(r_1 + r_2)^2 K_1 K_2}{4(r_1 K_2 + r_2 K_1)}. \tag{3.5}$$

The equilibria attained by the stock are the same in both sites:

$$N^1_{S,opt} = \frac{c_{S,opt}}{pq} = \frac{(r_1 + r_2)K_1K_2}{2(r_1K_2 + r_2K_1)} = N^2_{S,opt}.$$

Due to different biological parameters in the two sites, the equilibrium attained by the effort in each site is different

$$E^1_{S,opt} = \frac{r_1}{q}\left(1 - \frac{c_{S,opt}}{pqK_1}\right) = \frac{r_1}{q}\left(1 - \frac{(r_1 + r_2)K_2}{2(r_1K_2 + r_2K_1)}\right),\ E^2_{S,opt} = \frac{r_2}{q}\left(1 - \frac{(r_1 + r_2)K_1}{2(r_1K_2 + r_2K_1)}\right).$$

In the previous case of connected sites we showed that the MSY (3.4) is strongly dependent on equilibrium stock distribution. We found that to maximize MSY this distribution must be the IFD. In this case of unconnected sites the equilibrium stock distribution does not apply because they are independent. Nevertheless, we are showing that the way in which the total carrying capacity of the system, $K = K_1 + K_2$, is distributed between the sites does play a relevant role.

We start approaching the question in a simple case. Let us assume $r_1 = r_2 = r$, and represent the total carrying capacity distribution by means of the fraction $\alpha \in (0,1)$ of K in the first site, *i.e.*, $K_1 = \alpha K$ and $K_2 = (1-\alpha)K$. Substituting these values in (3.5) we get

$$Y_{S,opt} = \alpha(1-\alpha)rK,$$

which attains the well known maximum $\frac{1}{4}rK$ for $\alpha = \frac{1}{2}$, that is, when there is half of the total carrying capacity in each site. On the other hand, if K tends to be mostly in one of the sites the MSY approaches zero.

In the general case, $r_1 \neq r_2$, the MSY as a function of α is

$$Y_{S,opt}(\alpha) = \frac{(r_1+r_2)^2 K\alpha(1-\alpha)}{4(r_1(1-\alpha)+r_2\alpha)}.$$

This function also tends to zero when α tends to zero or one. Its maximum is attained for

$$\alpha = \frac{\sqrt{r_1}}{\sqrt{r_1}+\sqrt{r_2}},$$

that is, when the carrying capacities of the sites are proportional to the square roots of the corresponding intrinsic growth rates. If this is the case, the maximum yield is

$$Y_{S,opt}\Big(\frac{\sqrt{r_1}}{\sqrt{r_1}+\sqrt{r_2}}\Big) = \frac{1}{4}\left(\frac{r_1+r_2}{\sqrt{r_1}+\sqrt{r_2}}\right)^2 K.$$

where $\left(\frac{r_1+r_2}{\sqrt{r_1}+\sqrt{r_2}}\right)^2$ is in between r_1 and r_2.

Uniform costs in separated sites seem reasonable if the carrying capacities ratio is close to the ratio of the square roots of the intrinsic growth rates.

3.3. Comparison of the MSY for connected and unconnected sites

To compare the MSY obtained in the two cases, connected and unconnected sites, we define the ratio ρ_Y of Y_{opt} (3.4) to $Y_{S,opt}$ (3.5),

$$\rho_Y = \frac{Y_{opt}}{Y_{S,opt}} = \frac{(r_1K_2+r_2K_1)(r_1u_1+r_2u_2)^2}{(r_1+r_2)^2(r_2u_2^2K_1+r_1u_1^2K_2)}. \tag{3.6}$$

If $\rho_Y > 1$ then we can conclude that the movements increase the MSY whereas $\rho_Y < 1$ indicates that the movements reduce the MSY.

We can remark that ρ_Y depends only on the biological parameters, r_i and K_i, and the equilibrium stock distribution given by frequencies u_1 and $u_2 = 1-u_1$. On the other hand, it does not depend on the efforts frequencies v_i, that is, changing the efforts movements rates will not change ρ_Y.

As we pointed out in Section 3.1, the MSY in the case of connected sites attains its maximum when the equilibrium stock distribution coincides with IFD. The value of ρ_Y in this case ($u_1 = K_1/(K_1+K_2)$) can be expressed in the following form:

$$\rho_Y^{IFD} = \frac{(r_1+r_2)^2K_1K_2 + r_1r_2(K_1-K_2)^2}{(r_1+r_2)^2K_1K_2},$$

therefore, $\rho_Y^{IFD} > 1$ except in the case of equal carrying capacities, $K_1 = K_2$, in which it is equal to 1.

If the stock movements tend to IFD, the system with connected sites gives a larger MSY than the one with unconnected sites. If IFD is not the equilibrium of stock movements then this is not always the case.

Considering ρ_Y as a function of u_1 it is straightforward to find the conditions for $\rho_Y > 1$ to hold. Solving the equation $\rho_Y(u_1) = 1$ we obtain two solutions

$$\frac{1}{2} \quad \text{and} \quad \bar{u}_1 := \frac{(r_1 + 2r_2)K_1 - r_2 K_2}{2(r_2 K_1 + r_1 K_2)}.$$

Depending on $K_1 > K_2$, or $K_1 < K_2$, the second root satisfies $\bar{u}_1 > 1/2$, or $\bar{u}_1 < 1/2$, and we have then $\rho_Y > 1$ if and only if one of the next two conditions is met

$$K_1 > K_2 \text{ and } u_1 \in \left(\frac{1}{2}, \min\{\bar{u}_1, 1\}\right) \tag{3.7}$$

$$K_1 < K_2 \text{ and } u_1 \in \left(\max\{\bar{u}_1, 0\}, \frac{1}{2}\right) \tag{3.8}$$

We illustrate the results obtained with Figure 2.

To do it, we first express ρ_Y in terms of the ratio between K_1 and K_2, $\rho_K = K_1/K_2$, and the ratio between r_1 and r_2, $\rho_r = r_1/r_2$, getting

$$\rho_Y = \left(\frac{\rho_r u_1 + u_2}{\rho_r + 1}\right)^2 \frac{\rho_r + \rho_K}{\rho_r u_1^2 + \rho_K u_2^2}. \tag{3.9}$$

If both sites have equal carrying capacities, $K_1 = K_2$, *i.e.*, $\rho_K = 1$, we have

$$\rho_Y = \left(\frac{\rho_r u_1 + u_2}{\rho_r + 1}\right)^2 \frac{\rho_r + 1}{\rho_r u_1^2 + u_2^2} = \frac{(\rho_r u_1 + u_2)^2}{(\rho_r u_1 + u_2)^2 + \rho_r(u_1 - u_2)^2},$$

then $\rho_Y = 1$ for $u_1 = 1/2 = u_2$ and is less than 1 for any other value of u_1. Figure 2a shows the value of ρ_Y as a function of u_1 ($u_2 = 1 - u_1$) for $\rho_K = 1$ and different values of ρ_r.

The rest of the figures in Figure 2 make this same representation for three increasing values of ρ_K. In them one can clearly see the range of values of u_1 (3.7), the fraction of the stock that stabilizes in site 1, for which $\rho_Y > 1$, *i.e.*, for which the optimal yield is higher if the sites are connected. It can be seen that in all cases the maximum of ρ_Y is approximately reached when u_1 represents the IFD, that is, for $u_1 = \rho_K/(1 + \rho_K)$. We note that to obtain $\rho_Y > 1$ it is necessary for the equilibrium stock distribution to have more weight in the site with the highest carrying capacity. In Figure 2 we see that for any $u_1 < 1/2$ the site connection does not improve the maximum yield, *i.e.*, $\rho_Y < 1$. Concerning the role of the intrinsic growth ratio, ρ_r, we observe that the maximum value of ρ_Y, for fixed ρ_K, is obtained for $\rho_r = 1$, that is, when $r_1 = r_2$.

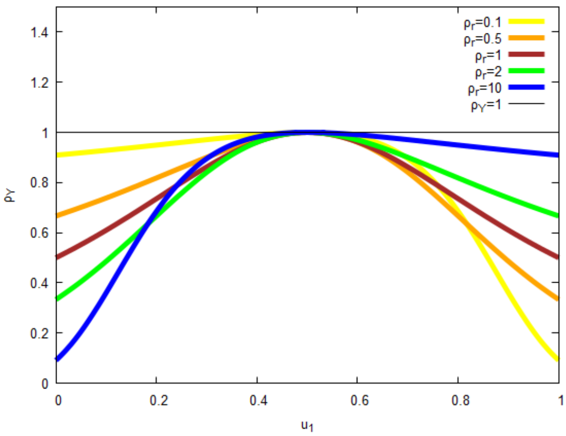
4. An L-site harvested population model ($L > 2$)

In this section we extend the analysis carried out in Section 3 to a general multisite environment encompassing L different sites.

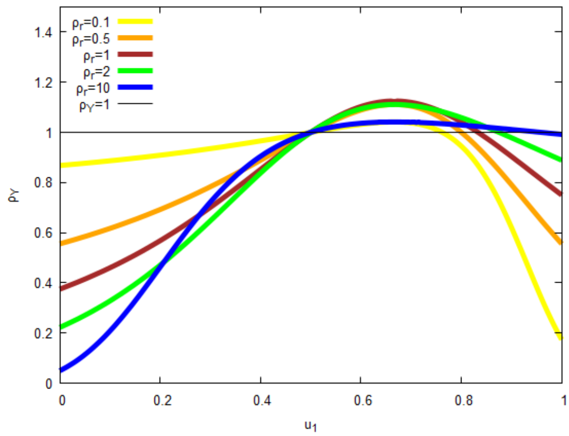
We continue to consider a harvested population and are interested in comparing the maximum sustainable yield between the case with connected sites and the case with isolated sites.

In each site, the stock-effort dynamics is ruled by a local basic Gordon-Schaefer model (2.1).

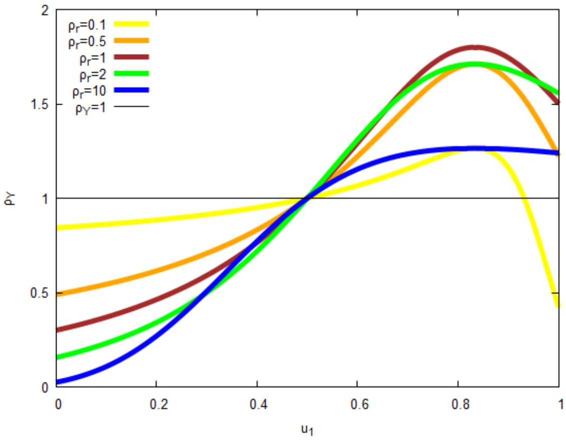
In the case of connected sites, we assume that movements between sites are fast compared to local dynamics. They are described by constant rates. Let us denote m_{ij} and μ_{ij}, $i \neq j$ and $i, j \in \{1, \ldots, L\}$, the transition rates



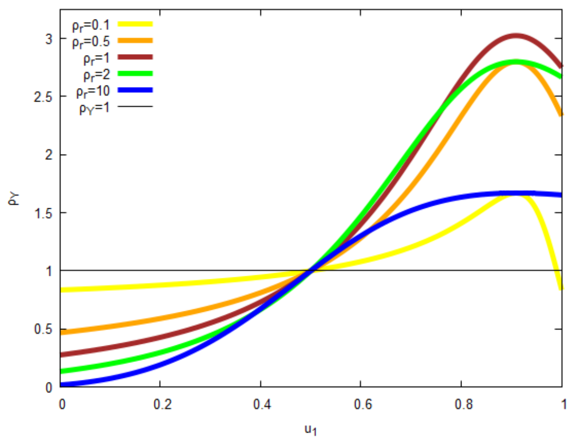
(A) $\rho_K = 1$



(B) $\rho_K = 2$



(C) $\rho_K = 5$



(D) $\rho_K = 10$

FIGURE 2. Graphs of ρ_Y as a function of u_1 for different values of ρ_K: 1, 2, 5, and 10; and different values of ρ_r: 0.1, 0.5, 1, 2, and 10.

from site j to site i, for stock and effort respectively. To ease the model writing, let us define, for $i \in \{1, \ldots, L\}$,

$$m_{ii} = - \sum_{\substack{j = 1 \\ j \neq i}}^{L} m_{ji} \quad , \qquad \mu_{ii} = - \sum_{\substack{j = 1 \\ j \neq i}}^{L} \mu_{ji}.$$

They represent the rate at which stock or effort leave site i to go to the rest of sites.

The extension of model (3.1) to an L-site environment reads as follows:

$$\begin{aligned} \frac{\mathrm{d}N_i}{\mathrm{d}\tau} &= \sum_{j=1}^{L} m_{ij}N_j + \varepsilon\Big(r_iN_i\Big(1-\frac{N_i}{K_i}\Big) - qE_iN_i\Big), \\ \frac{\mathrm{d}E_i}{\mathrm{d}\tau} &= \sum_{j=1}^{L} \mu_{ij}E_j + \varepsilon\big(pqE_iN_i - cE_i\big) \qquad , \ i=1,\dots,L. \end{aligned} \tag{4.1}$$

where, N_i and E_i are the population density and the fishing effort on site i. Parameters r_i and K_i represent the intrinsic growth rate and the carrying capacity, respectively, on site i. The catchability q, the price per harvest unit p and the cost per unit effort c are still assumed to be equal in all sites. The fast time variable is τ and positive parameter $\varepsilon \ll 1$ represents the time scales ratio.

In the case of unconnected sites, as there is no stock and effort movements, the dynamics is represented by the following independent systems, for $i = 1, \dots, L$:

$$\begin{aligned} \frac{\mathrm{d}N_i}{\mathrm{d}t} &= r_iN_i\Big(1-\frac{N_i}{K_i}\Big) - qE_iN_i \\ \frac{\mathrm{d}E_i}{\mathrm{d}t} &= pqE_iN_i - cE_i \end{aligned} \tag{4.2}$$

Assuming that matrices $M_1 = (m_{ij})$ and $M_2 = (\mu_{ij})$ are irreducible, the same method we used to reduce system (3.1), [3, 4], apply to system (4.1). The interpretation of the irreducibility of a matrix in this context is that the connections between sites allow to establish a path joining any site to any other. The movements dynamics leave the total stock $N = N_1 + \cdots + N_L$ and the total fishing effort $E = E_1 + \cdots + E_L$ invariant. Moreover, it makes the proportions of stock and effort in each site rapidly tend to an equilibrium. Let $\bar{u} = (u_1, \dots, u_L)$ and $\bar{v} = (v_1, \dots, v_L)$ be these equilibrium proportions for stock and effort respectively. Vectors $\bar{u}$ and $\bar{v}$ are the right eigenvectors of matrices M_1 and M_2 associated to eigenvalue 0 and whose entries sum up to 1, see Section A.5. in [24] for details on this kind of matrices called quasipositive irreducible.

The associated reduced system for the total stock and effort in terms of the slow time variable $t = \varepsilon\tau$ is the following basic Gordon-Schaefer model:

$$\begin{aligned} \frac{\mathrm{d}N}{\mathrm{d}t} &= \sum_{i=1}^{L}\Big(r_iu_iN\Big(1-\frac{u_iN}{K_i}\Big) - qv_iEu_iN\Big) = \bar{r}N\Big(1-\frac{N}{\bar{K}}\Big) - \bar{q}EN \\ \frac{\mathrm{d}E}{\mathrm{d}t} &= \sum_{i=1}^{L}\Big(pqv_iEu_iN - cv_iE_i\Big) = p\bar{q}EN - cE \end{aligned} \tag{4.3}$$

where

$$\bar{r} = \sum_{i=1}^{L} u_ir_i \quad , \qquad \bar{K} = \frac{\bar{r}}{\displaystyle\sum_{i=1}^{L}\big(u_i^2\frac{r_i}{K_i}\big)} \quad , \qquad \bar{q} = \Big(\sum_{i=1}^{L}(u_iv_i)\Big)q. \tag{4.4}$$

To compare the maximum sustainable yield in the cases of connected and unconnected sites, we now consider the yield at equilibrium maximized as a function of a single cost. In the first case using system (4.3) and in the second case with the help of systems (4.2).

4.1. Connected sites

In the case of connected sites, we apply (2.4), the value of the cost that maximizes the equilibrium yield in the basic Gordon-Schaefer model, to system (4.3), obtaining

$$c_{opt} = \frac{1}{2} p\bar{q}\bar{K},$$

and the maximum equilibrium yield

$$Y_{opt} = \frac{1}{4}\bar{r}\bar{K} = \frac{1}{4} \frac{\left(\sum_{i=1}^{L} u_i r_i\right)^2}{\sum_{i=1}^{L}(u_i^2 r_i/K_i)}. \tag{4.5}$$

It does not depend on either the price, the catchability or the efforts movements rates. On the other hand, it is strongly dependent on the equilibrium stock distribution. Let us show this through a simple extreme case as we did in the case of two sites. Assuming biologically identical sites, $r_i = r$ and $K_i = K/L$, for $i = 1, \ldots, L$, then we have

$$Y_{opt} = \frac{rK}{4} \cdot \frac{1}{L\sum_{i=1}^{L} u_i^2}.$$

If the stock is homogeneously distributed, $u_i = 1/L$, then $Y_{opt} = rK/4$, that corresponds to the MSY considering a single stock with biological parameters r and K. Nevertheless, if the stock tends to concentrate in a single site, let us think that u_1 approaches 1 and u_i approaches 0 for $i = 2, \ldots, L$, then Y_{opt} tends to $rK/(4L)$, *i.e.*, the previous maximum yield is divided by the number of sites.

If we now consider Y_{opt} as a function of variables u_i $(i = 1, \ldots, L)$ we can prove that the maximum of Y_{opt} is obtained for a distribution that corresponds to IFD, *i.e.*, $u_i = K_i/\sum_{j=1}^{L} K_j$. To see it, let us consider function $Y_{opt}(u_1, \ldots, u_L)$ with the constraint $u_1 + \cdots + u_L = 1$, $u_i > 0$, and use a Lagrange multiplier λ. For $j = 1, \ldots, L$,

$$\lambda = \frac{\partial Y_{opt}}{\partial u_j} = \frac{1}{4}\bar{r}\bar{K} = \frac{1}{2} r_j \bar{K} - \frac{1}{2}\bar{K}^2 \frac{u_j r_j}{K_j},$$

multiplying each equality by u_j and summing up all of them yields

$$\lambda = \sum_{j=1}^{L} u_j \left(\frac{1}{2} r_j \bar{K} - \frac{1}{2}\bar{K}^2 \frac{u_j r_j}{K_j}\right) = \frac{1}{2}\bar{r}\bar{K} - \frac{1}{2}\bar{K}^2 \frac{\bar{r}}{\bar{K}} = 0,$$

substituting $\lambda = 0$ in the first equality gives

$$u_j = \frac{K_j}{\bar{K}},$$

and, as $u_1 + \cdots + u_L = 1$, $\bar{K} = K_1 + \cdots + K_L$. So, as we wanted to prove, the stock distribution that maximizes Y_{opt} is the IFD. This yield value is

$$Y_{opt}^{IFD} = Y_{opt}(K_1/\bar{K}, \ldots, K_L/\bar{K}) = \frac{1}{4}\sum_{i=1}^{L} r_i K_i,$$

and it is associated to a cost $c_{opt} = \frac{1}{2} pq \sum_{i=1}^{L} r_i K_i$ at an equilibrium

$$N_{opt} = \frac{1}{2}\sum_{i=1}^{L} K_i \quad \text{and} \quad E_{opt} = \Big(\sum_{i=1}^{L} r_i K_i\Big) / \Big(2q\sum_{i=1}^{L} v_i K_i\Big).$$

4.2. Unconnected sites

When the sites are not connected we must consider them independently. Thus, the yield of the system is just the sum of the yields on each separate site. Using expression (2.3) in all the L systems (4.2), one gets:

$$Y_S = \sum_{i=1}^{L} \frac{r_i c}{pq}\Big(1 - \frac{c}{pqK_i}\Big) = \frac{c}{pq}\sum_{i=1}^{L} r_i - \frac{c^2}{p^2q^2}\sum_{i=1}^{L}\frac{r_i}{K_i}$$

We look for a common value of c that optimizes Y_S. Considering Y_S as a function of c, the maximum is attained at

$$c_{S,opt} = \frac{1}{2} pq \Big(\sum_{i=1}^{L} r_i\Big) / \Big(\sum_{i=1}^{L} r_i/K_i\Big),$$

and the maximum yield is equal to

$$Y_{S,opt} = \Big(\sum_{i=1}^{L} r_i\Big)^2 / \Big(4\sum_{i=1}^{L}\frac{r_i}{K_i}\Big). \tag{4.6}$$

The equilibria attained by the stock is the same in every site $j = 1, \ldots, L$

$$N_{S,opt}^{j} = \frac{1}{2}\Big(\sum_{i=1}^{L} r_i\Big) / \Big(\sum_{i=1}^{L} r_i/K_i\Big),$$

but this need not be the case concerning the effort equilibria

$$E_{S,opt}^{j} = \frac{r_j}{q}\left(1 - \Big(\sum_{i=1}^{L} r_i\Big) / \Big(2K_j\sum_{i=1}^{L} r_i/K_i\Big)\right).$$

In the previous case of connected sites we showed that the MSY (4.5) is strongly dependent on equilibrium stock distribution associated to stock fast movements. When this distribution is the IFD the maximum equilibrium yield attains its maximum. In the case of unconnected sites movements are not considered and, therefore, it does not make sense to speak about the equilibrium stock distribution they lead to. Nevertheless, we can consider the distribution among sites of the total carrying capacity of the system, $K = \sum_{i=1}^{L} K_i$, and show that it does play a relevant role by treating a simple case.

Assuming, equal intrinsic growth rates in all sites, $r_i = r$ for $i = 1, \dots, L$, and setting $K_i = \alpha_i K$, with $\alpha_i \in (0, 1)$, we have

$$Y_{S,opt} = \Big(\sum_{i=1}^{L} r\Big)^2 / \Big(4 \sum_{i=1}^{L} \frac{r}{\alpha_i K}\Big) = \frac{1}{4} rKL \frac{L}{\sum_{i=1}^{L} 1/\alpha_i},$$

where the term $L/\sum_{i=1}^{L} 1/\alpha_i$ is the harmonic mean of the constants α_i. As the harmonic mean is always less than or equal to the arithmetic mean we have that

$$Y_{S,opt} \leq \frac{1}{4} rK,$$

with the equality obtained if all sites share the same carrying capacity, *i.e.*, $\alpha_i = 1/L$ for all $i = 1, \dots, L$. On the other hand, it can be noted that if one of the constants α_i tends to zero then so does the harmonic mean of all, what entails the $Y_{S,opt}$ also tending to zero.

Uniform cost in separated sites with very different carrying capacities would lead to small $Y_{S,opt}$.

If we treat the general case with possibly different local intrinsic growth rates r_i, we obtain analogous results to those found in the model with two sites. Let us set, as above, $K_i = \alpha_i K$, with $\alpha_i \in (0, 1)$, and consider $Y_{S,opt}$ as a function of variables α_i $(i = 1, \dots, L)$. To calculate its maximum we can use function $Y_{S,opt}(\alpha_1, \dots, \alpha_L)$ with the constraint $\alpha_1 + \cdots + \alpha_L = 1$, $\alpha_i > 0$, and use a Lagrange multiplier λ. For $j = 1, \dots, L$,

$$\lambda = \frac{\partial Y_{S,opt}}{\partial \alpha_j} = \frac{K}{4} \cdot \frac{\big(\sum_{i=1}^{L} r_i\big)^2}{\big(\sum_{i=1}^{L} (r_i/\alpha_i)\big)^2} \cdot \frac{r_j}{\alpha_j^2},$$

which implies that α_j is proportional to $\sqrt{r_j}$

$$\alpha_j = \frac{1}{2} \sqrt{\frac{K}{\lambda}} \cdot \frac{\sum_{i=1}^{L} r_i}{\sum_{i=1}^{L} (r_i/\alpha_i)} \sqrt{r_j}$$

and, therefore, for $j = 1, \dots, L$,

$$\alpha_j = \frac{\sqrt{r_j}}{\sum_{i=1}^{L} \sqrt{r_i}}.$$

If the carrying capacities K_i of the sites are proportional to the square roots of the corresponding intrinsic growth rates $\sqrt{r_i}$ then $Y_{S,opt}$ attains its maximum

$$Y_{S,opt}\Big(\frac{\sqrt{r_1}}{\sum_{i=1}^{L} \sqrt{r_i}}, \cdots, \frac{\sqrt{r_L}}{\sum_{i=1}^{L} \sqrt{r_i}}\Big) = \frac{1}{4} K \left(\frac{\sum_{i=1}^{L} r_i}{\sum_{i=1}^{L} \sqrt{r_i}}\right)^2.$$

4.3. Comparison of Y_{opt} and $Y_{S,opt}$

To compare the maximum yield as obtained in the two studied cases, connected and unconnected sites, we define the ratio ρ_Y of Y_{opt} (4.5) to $Y_{S,opt}$ (4.6),

$$\rho_Y = \frac{Y_{opt}}{Y_{S,opt}} = \frac{\left(\sum_{i=1}^{L} u_i r_i\right)^2 \sum_{i=1}^{L} (r_i/K_i)}{\left(\sum_{i=1}^{L} r_i\right)^2 \sum_{i=1}^{L} (u_i^2 r_i/K_i)}. \tag{4.7}$$

If $\rho_Y > 1$, fast movements increase the maximum yield whereas $\rho_Y < 1$ indicates that movements reduce it.

As it was remarked in the model with two sites, ρ_Y depends only on the biological parameters, r_i and K_i, and on the stock movements through the equilibrium stock distribution u_i, but it does not depend on the efforts frequencies v_i. Changing the efforts movements rates will not change the value of ρ_Y.

As we pointed out in Section 4.1, the maximum yield in the case of connected sites is obtained when the equilibrium stock distribution coincides with IFD. The value of ρ_Y in this case ($u_i = K_i/\sum_{i=1}^{L} K_i$, $i = 1, \ldots, L$) is the following:

$$\rho_Y^{IFD} = \frac{\sum_{i=1}^{L}(r_i K_i)\sum_{i=1}^{L}(r_i/K_i)}{\left(\sum_{i=1}^{L} r_i\right)^2}.$$

Using that function $f(x) = x + 1/x$ satisfies $f(x) > 2$ for $x \in (0,1) \cup (1,\infty)$ and $f(1) = 2$, we have, for any $i, j = 1, \ldots, L$,

$$\frac{K_i}{K_j} r_i r_j + \frac{K_j}{K_i} r_j r_i > r_i r_j + r_j r_i \text{ if } K_i \neq K_j, \tag{4.8}$$

and the equality of both expressions holds if $K_i = K_j$. Now, as we can write ρ_Y^{IFD} in the following form

$$\rho_Y^{IFD} = \frac{\sum_{i=1}^{L}\sum_{j=i+1}^{L}\left(\frac{K_i}{K_j} r_i r_j + \frac{K_j}{K_i} r_j r_i\right) + \sum_{i=1}^{L} r_i^2}{\sum_{i=1}^{L}\sum_{j=i+1}^{L}(r_i r_j + r_j r_i) + \sum_{i=1}^{L} r_i^2},$$

we obtain that $\rho_Y^{IFD} > 1$ except in the case of equal carrying capacities, $K_i = K_j$ for all $i, j \in \{1, \ldots, L\}$, in which it is equal to 1.

If the stock movements tend to IFD, the system with connected sites gives a larger maximum yield than the one obtained with unconnected sites. If IFD is not the equilibrium of stock movements then this is not always the case. It does not seem straightforward to find necessary and sufficient conditions for ρ_Y being bigger or less than 1. To show that unconnected sites can also lead to a larger maximum yield, let us calculate ρ_Y in the simple case with equal intrinsic growth rates and equal carrying capacities (ECC) in all sites. Let $r_i = r$ and $K_i = K/L$ for $i = 1, \ldots, L$, where K represents the total carrying capacity. The ρ_Y, in this case, is readily calculated to be

$$\rho_Y^{ECC} = \frac{1}{L\sum_{i=1}^{L} u_i^2}.$$

As $u_i \geq 0$ and $\sum_{i=1}^{L} u_i = 1$, it is straightforward to find that $1/L \leq \sum_{i=1}^{L} u_i^2 \leq 1$ and, thus,

$$\frac{1}{L} \leq \rho_Y^{ECC} \leq 1.$$

In this case, equal intrinsic growth rates and equal carrying capacities, the system with unconnected sites gives a larger maximum yield than the one obtained with connected sites. If stock movements tend to IFD, then ρ_Y approaches 1, but it can be much less than 1 if stock movements equilibrium distribution gets away from IFD.

5. Conclusion

Multi-site models, often reduced to only two sites, are commonly used in ecology, epidemiology or the so-called eco-epidemiology, see [20] as an example in this last field. In strong relation with our work, within the multi-site models in ecology, the early contribution [14] showed that the global carrying capacity of two sites connected by fast migrations where each sub-population grows logistically could be globally greater than the sum of the carrying capacities of the two isolated sites. This result has received a lot of attention recently and has been discussed in several other articles, [1, 2, 11, 12, 17, 21, 25]. A condition for obtaining higher productivity from the system of two connected sites compared to the system of two isolated sites is to consider a heterogeneous environment, that is to say with two sites having different environmental properties, in particular having different growth rates and carrying capacities, [21].

In this work we have analyzed a similar problem. We have treated a population that grows according to the logistic model but that, in addition, is harvested. The actual system we have in mind is a fishery. The environment of the population can be considered divided into different sites, that is, we are dealing with the case of a multisite fishery. Finally, what we seek to compare between the system of connected and unconnected sites is not the total carrying capacity of the system, as in the works mentioned above, but the maximum sustainable yield.

This problem, as we mentioned in the introduction, has already been dealt with in [5]. As can be seen in system (1.2), the population is harvested at a rate proportional to its size following the classical Schaefer's model. Yield optimization is performed with respect to the fishing effort parameter E. The analysis of the model offers a result that we could describe as negative. Regardless of the movement rates chosen and whether or not the sites are environmentally homogeneous, connecting the sites does not allow increasing the sum of the MSY of the unconnected sites. Equality occurs when the exploited species is distributed over the two sites according to the ideal free distribution. This result is quite general as soon as the harvested population equation includes a logistic growth term from which the catch is subtracted. Indeed, at equilibrium, the capture is equal to a logistic growth term which is always maximum when the population is at half the carrying capacity. This always leads to the same value of the catch at MSY and, therefore, to the inability to increase optimal yield by connecting sites. A positive answer is obtained in the same work [5] considering a prey−predator community of fish in the same environment, where only the predators are harvested. It is shown that the total MSY of the system can be greater with connected sites. The condition leading to this result consist in connecting a fishing site with a large prey carrying capacity and an average growth rate to a site with a small prey carrying capacity but a large growth rate.

The models analyzed in this paper includes economic factors, which were not considered in [5]. The fishing effort E becomes a variable whose dynamics follow the hypothesis of the open access fishery. The non-spatialized model, (2.1), leads, under a certain condition, to an equilibrium of both the stock and the effort, and therefore also the yield. From this, we have chosen the cost c as a parameter with respect to which to optimize the yield. We have preferred c over other possible choices because it includes all the costs of operating a fishery, including the profit margin that the owner considers profitable. In addition, it is an element on which management can act through taxes or subsidies.

The model (2.1) is used as a local model to build a multisite fishery model. The management of the fishery is unique and the same cost and price are established in each of the sites. When unconnected sites are considered, the model for the fishery is made up of a collection of independent systems (2.1). When the sites are connected, with rapid movements of the stock and of the fishing effort, the model (3.1) is proposed for two sites and, in general, for any number L of sites, the model (4.1). Once the maximum sustainable yield (MSY) is obtained based on the cost c, the comparison between the fishery with connected and unconnected sites based on this criterion is developed. The ratio ρ_Y between the MSY with connected sites, Y_{opt}, and with unconnected sites, $Y_{S,opt}$, is used to decide whether to prefer a connected fishery, if $\rho_Y > 1$, or an unconnected fishery, whenever $\rho_Y < 1$.

In the case of two sites the ratio ρ_Y depends on two other ratios, that of the carrying capacities, ρ_K, and that of the intrinsic growth rates, ρ_r, and on the equilibrium distribution of the stock reflected in u_1. The rest of the parameters do not play any role. A first general conclusion is that if the carrying capacities of the two sites are equal, $\rho_K = 1$, then for any values of u_1 and ρ_r we have that $\rho_Y \leq 1$, with the equality valid only if $u_1 = 1/2$. If the two sites have the same carrying capacities, it is better to keep the sites unconnected. Another general result but in the opposite sense follows. If the equilibrium distribution of the stock coincides with the IFD then it is better to use connected sites. Figure 2 shows that whenever the carrying capacity of site 1 is greater than that of site 2, $\rho_K > 1$, there is an interval of values of u_1, whose left endpoint is $1/2$ and, on the right, can be as high as 1, such that $\rho_Y > 1$. If the fishery can be managed so that the equilibrium distribution of the stock is in this interval, connecting the sites will give a higher MSY. Note that the best results are obtained when the equilibrium distribution of the stock is around the IFD. The values of ρ_Y obtained grow with ρ_K and are reached for values of ρ_r close to 1, *i.e.* equal intrinsic growth rates. A symmetric analysis is valid if the largest carrying capacity is that of site 2. Similar general conclusions can be reached in the case of L sites.

This work shows the importance of maintaining corridors allowing individuals to move from one site to another in a network of sites. It also shows that the heterogeneity between the different sites is a favorable factor for the increase in the total optimal catch in the multisite fishery. This work makes it possible to specify the conditions favorable to this increase in the capture at the MSY. The manager of the multisite fishery can use certain devices such as artificial reefs to increase the total productivity of the multisite fishery. In the case of two connected fishing areas, it would be possible to increase the carrying capacity in only one of the two zones by installing artificial reefs there, which are known to increase the productivity of the halieutic resource by increasing the local carrying capacity. Artificial reefs have a priori no effect on the growth rate of the exploited species. Thus it appears possible to create an asymmetry between the fishing zones by increasing the ratio of local carrying capacities ρ_K while maintaining the ratio of growth rates ρ_r at one. Figure 2 shows that it is possible as soon as ρ_K is equal to 2 or more to obtain $\rho_Y \geq 1$.

In [26], the authors performed experiments with aquatic plants growing logistically in containers. They simulated in real world the fast migrations by transferring plants from one container to another with a periodicity of a few days. They considered a heterogeneous environment with different growth conditions from container to container of different sizes. Under these conditions, they showed that the total productivity, in terms of carrying capacities, could be greater in heterogeneous conditions rather than in homogeneous conditions. An important perspective of this work is to consider carrying out experiments of the same type making it possible to generalize the results obtained in [26] to the case of exploited species, either a single commercial species as in this work with an identical operating cost in all sites or in the case of fish prey-predator systems with exploitation of the predator, [5].

Acknowledgements. Rafael Bravo de la Parra is supported by Ministerio de Universidades (Spain) with grant PRX21/00034 in the Programa Estatal de Promoción del Talento y su Empleabilidad en I+D+i, Subprograma Estatal de Movilidad, of the Plan Estatal de Investigación Científica y Técnica y de Innovación 2017-2020.

References

[1] R. Arditi, C. Lobry and T. Sari, Is dispersal always beneficial to carrying capacity? New insights from the multi-patch logistic equation. *Theor. Pop. Biol.* **106** (2015) 45–59.

[2] R. Arditi, C. Lobry and T. Sari, Asymmetric dispersal in the multi-patch logistic equation. *Theor. Pop. Biol.* **120** (2018) 11–15.

[3] P. Auger, R. Bravo de la Parra, J.-C. Poggiale, E. Sánchez and N.T. Huu, Aggregation of variables and applications to population dynamics, in P. Magal and S. Ruan (Eds.), Structured Population Models in Biology and Epidemiology. Vol. 1936 of *Lecture Notes in Mathematics. Math. Biosci. Subseries.* Springer (2008) pp. 209–263.

[4] P. Auger, R. Bravo de la Parra, J.-C. Poggiale, E. Sánchez and L. Sanz, Aggregation methods in dynamical systems and applications in population and community dynamics. *Phys. Life. Rev.* **5** (2008) 79–105.

[5] P. Auger, B. Kooi and A. Moussaoui, Increase of maximum sustainable yield for fishery in two patches with fast migration. *Ecol. Model.* **467** (2022) 109898.

[6] C. Bernstein, P. Auger and J.-C. Poggiale, Predator migration decisions, the ideal free distribution, and predator-prey dynamics. *Am. Nat.* **153** (1999) 267–281.

[7] S.A. Bortone, Resolving the attraction-production dilemma in artificial reef research: some Yeas and Nays. *Fisheries* **23** (1998) 6–10.

[8] T. Brochier, P. Brehmer, A. Mbaye, M. Diop, N. Watanuki, H. Terashima, D. Kaplan and P. Auger, Successful artificial reefs depend on getting the context right due to complex socio-bio-economic interactions. *Sci. Rep.-UK* **11** (2021) 16698.

[9] C.W. Clark, Mathematical Bioeconomics. The Optimal Management of Renewable Resources. John Wiley & Sons (1990).

[10] L. Dagorn, K.N. Holland and D.G. Itano, Behavior of yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna in a network of fish aggregating devices (FADs). *Mar. Biol. (Berl.)* **151** (2007) 595–606.

[11] D.L. DeAngelis, W.-M. Ni and B. Zhang, Effects of diffusion on total biomass in heterogeneous continuous and discrete-patch systems. *Theor. Ecol.* **9** (2016) 443–453.

[12] D.L. DeAngelis and B. Zhang, Effects of dispersal in a non-uniform environment on population dynamics and competition: a patch model approach. *Discrete Contin. Dyn.-B* **19** (2014) 3087–3104.

[13] A. Fonteneau, J. Ariz, D. Gaertner, T. Nordstrom and P. Pallares, Observed changes in the species composition of tuna schools in the Gulf of Guinea between 1981 and 1999, in relation with the fish aggregating device fishery. *Aquat. Living Resour.* **13** (2000) 253–257.

[14] H.I. Freedman and D. Waltman, Mathematical models of population interactions with dispersal. I. Stability of two habitats with and without a predator. *SIAM J. Appl. Math.* **32** 1977 631–648.

[15] S.D. Fretwell and H.L. Lucas, On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* **19** (1970) 16–36.

[16] R. Hilborn, F. Michel and G.A. De Leo, Integrating marine protected areas with catch regulation. *Can. J. Fish. Aquat. Sci.* **63** (2006) 642–649.

[17] R.T. Holt, Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat. *Theor. Pop. Biol.* **28** (1985) 181–208.

[18] M. Iannelli and A. Pugliese, An Introduction to Mathematical Population Dynamics. Along the trail of Volterra and Lotka. Springer (2014).

[19] C. Jerry and N. Raïssi, Optimal exploitation for a commercial fishing model. *Acta Biotheor.* **60** (2012) 209–223.

[20] T. Moulin, A. Perasso and E. Venturino, A metaecoepidemic model of grassland ecosystem with only consumers' migration. *B. Math. Biol.* **82** (2020) 88.

[21] J.-C. Poggiale, P. Auger, D́. Nerini, C. Manté and F. Gilbert, Global production increased by spatial heterogeneity in a population dynamics model, *Acta Biotheor.* **53** (2005) 359–370.

[22] J.J. Polovina and I. Sakai, Impacts of artificial reefs on fishery production in Shimamaki, Japan. *Bull. Mar. Sci.* **44** (1989) 997–1003.

[23] M.B. Schaefer, Some considerations of population dynamics and economics in relation to the management of the commercial marine fisheries. *J. Fish. Res. Board Canada* **14** (1957) 669–681.

[24] H.L. Smith and H.R. Thieme, Dynamical Systems and Population Persistence. American Mathematical Society (2011).

[25] B. Zhang, D.L. DeAngelis and W.-M. Ni, Carrying capacity of spatially distributed metapopulations. *Trends Ecol. Evol.* **36** (2021) 164–173.

[26] B. Zhang, A. Kula, K.M.L. Mack, L. Zhai, A.L. Ryce, W.-M. Ni, D.L. DeAngelis and J.D. Van Dyken, Carrying capacity in a heterogeneous environment with habitat connectivity. *Ecol. Lett.* **20** (2017) 1118–1128.