Increase of maximum sustainable yield for fishery in two patches with fast migration

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ABSTRACT

We present a model of a fish population present on two patches connected by migrations. Fish grow logistically on each patch and are caught. We assume that migrations between the two sites are fast relative to local growth and fishing. Taking advantage of the time scales, we use methods of aggregation of variables to obtain a reduced model governing the total biomass of the fish population at a slow time scale. We are looking for the maximum sustainable yield (MSY) for the system of the two connected patches. We show that although the total equilibrium population may be greater than the sum of the carrying capacities on each isolated site, the total catch is always less than or equal to the sum of the catches on the isolated fishing sites. We then consider a prey–predator community of fish in the same environment. We assume that only the predator is caught and not its prey, growing logistically on each site. We study the Lotka–Volterra prey–predator model as well as the model with a type II Holling functional response. We show that the total catch at MSY of the system of connected sites can be greater than the sum of the captures on each isolated site. This result is obtained when a fishing site with a large prey carrying capacity and an average growth rate is connected to a site with a small carrying capacity but a large growth rate. Finally, we discuss fishery management methods on two fishing sites for the Lotka–Volterra model as well as the Holling type II model in the case of a prey refuge.

1. Introduction

Many authors have been interested in population dynamics in heterogeneous environments that can be represented by a set of discrete sites connected to each other by migratory flows. Particular interest was given to the study of the effects of migration on the global dynamics of the metapopulation, (Levin, 1974; DeAngelis and Zhang, 2014; DeAngelis et al., 2016). Many works have considered the case where the populations on each site obey a law of logistic growth. The 2-patch model and the generalization to a network of N sites ($N > 2$) have been studied. Most authors looked for the conditions allowing to have a global equilibrium greater than the sum of the carrying capacities of all the sites, (Holt, 1985; Freedman and Waltman, 1977; Poggiale et al., 2005; Arditi et al., 2015, 2018; Wang and DeAngelis, 2019; Elbetch et al., 2021).

On another side, many models of exploited populations have been studied, in particular in the field of fisheries, (Murray, 2002), a single harvested species as well as exploited prey–predator communities (Spencer and Collie, 1995b,a) with a ratio-dependent functional

response. A particularly important aspect concerns the optimal management of a fishery to ensure maximum profitability of the fishery, by looking for the conditions to reach the MSY, (Clark, 1990). Several authors have been interested in determining the MSY in various fish prey–predator communities, (Legovic and Gecek, 2010; Legovic et al., 2011; Legovic and Gecek, 2012; Ghosh and Kar, 2013; Kar and Ghosh, 2013).

Another aspect of fishery modeling concerns taking into account the heterogeneity of fishing zones. The heterogeneity of the fishery can be taken into account by considering a spatially continuous model with parameters of growth and interactions which depend on the position in space. Another way to do this is to consider separate and different fishing areas which can be connected together by migrations of various fish species as well as fishing fleets. It is this last approach that we adopt in this work.

We focus our approach on the case of fishing areas close enough so that the migrations of fish between areas can take place at a fast time scale compared to local population growth and capture. The existence

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of two time scales will allow us to reduce the dimension of the complete model taking into account all the growth and fishing terms on each site as well as the migration terms and to derive a reduced model governing only the total fish biomass of all sites at a slow time scale. These reduction methods make it possible to study the complete model using the simplified reduced model. In previous work, Poggiale et al. (2005) studied the case of a single logistically growing population at two sites connected by fast migrations. They showed that the total population of the two sites connected by fast migrations at constant rates could tend towards a stable equilibrium greater than the sum of the carrying capacities of the two isolated sites. This result shows that it is possible to increase the productivity of a population living on two sites by adequately connecting the two sites with migrations, (Poggiale et al., 2005). We generalize this last work by considering that the logistically growing local populations are moreover captured.

The question that arises in the general context of a fishery on two sites is to find out whether the total catch of the system of the two sites connected by migrations can be greater than the sum of the optimal catches of the two isolated sites, i.e. at MSY. Is there a way to make connections between fishing areas that increases the total catch of the fishery ? The first part of the present work concerns a single harvested population on two sites. In this first case, we show that the answer to the previous question is negative. We then address this issue in the case of a prey–predator community of fish from which only the predator is caught. We show that in this second case, the answer is positive. This part studies a fish prey–predator community with a type I functional response, the predator of which is always fished on two sites, as well as a fish community with a type II functional response. The last part focuses on the effects of connectivity of two fishing areas on the global productivity of the fishery with two suggested concrete application examples. The work ends with concluding remarks and perspectives.

2. A two-patch population model with logistic growth and constant fast migrations

2.1. Without harvesting

We start by recalling the result given in the following Poggiale et al. (2005) in which the authors considered a single population in a two-patch environment. In our case, we consider a fish population growing on two sites. The movements between patches are described by constant migration rates. Migrations are assumed to be fast in comparison to local dynamics. Let us recall the model:

$$\frac{dB_1}{d\tau} = m_2 B_2 - m_1 B_1 + \epsilon\left(r_1 B_1 (1 - \frac{B_1}{K_1})\right) \tag{1}$$

$$\frac{dB_2}{d\tau} = m_1 B_1 - m_2 B_2 + \epsilon\left(r_2 B_2 (1 - \frac{B_2}{K_2})\right) \tag{2}$$

where, for $i = 1, 2$, B_i are fish biomass on patch i. Parameters r_i and K_i represent the intrinsic growth rate and the carrying capacity on patch i. The migration rates, m_i, are constant. Time scales are included in the model by using the fast time variable τ together with the positive dimensionless parameter $\epsilon \ll 1$ that represents their ratio. t is the slow time such that $t = \epsilon\tau$.

The complete model can be reduced. As a first step, we consider the fast system which is obtained by setting $\epsilon = 0$ in the complete system. In our case, the fast equilibrium can be easily calculated and is given by:

$$B_1^* = uB = \frac{m_2}{m_1 + m_2} B \tag{3}$$

$$B_2^* = (1 - u)B = \frac{m_1}{m_1 + m_2} B \tag{4}$$

Where $u = \frac{m_2}{m_1 + m_2}$ represents the constant proportion of fish Biomass in patch 1 and $(1 - u)$ in patch 2 at the fast equilibrium. A reduced model is obtained by substituting the fast stable equilibrium into the

complete system. Adding two by two equations for fish biomass and by using slow time, we get the following aggregated model governing the total fish biomass $B = B_1 + B_2$ at the slow time which is valid when it is structurally stable and for small enough value of ϵ:

$$\frac{dB}{dt} = rB(1 - \frac{B}{K}) + O(\epsilon) \tag{5}$$

For reduction methods using small parameters, we refer to Tikhonov (1952). For aggregation of variables methods we refer to Iwasa et al. (1989). When the reduced system obtained by substituting the fast equilibrium in the complete model is not structurally stable, it is necessary to use reduction methods based on the center manifold theorem allowing following term of order ϵ to be calculated see Auger et al. (2008a) and Auger et al. (2008b).

With constant migration rates, the global aggregated equation is a logistic equation such as local equations. In the long term, B tends to the stable equilibrium $B^* = K$. The overall fish growth rate of the reduced model reads, (Poggiale et al., 2005):

$$r = ur_1 + (1 - u)r_2 \tag{6}$$

and the overall fish carrying capacity checks the next expression:

$$\frac{r}{K} = \frac{r_1 u^2}{K_1} + \frac{r_2 (1 - u)^2}{K_2} \tag{7}$$

and is expressed as follows:

$$K = \frac{K_1 K_2 (ur_1 + (1 - u)r_2)}{(u^2 K_2 r_1 + (1 - u)^2 K_1 r_2)} \tag{8}$$

In the homogeneous case, $r_1 = r_2$ and $K_1 = K_2$, the formula is simplified to give:

$$K_{Homogeneous} = \frac{K_1}{(u^2 + (1 - u)^2)} \tag{9}$$

In the case of symmetric diffusion $u = 0.5$, it is easy to check that $K_{Homogeneous,Sym} = 2K_1$. In the heterogeneous case and symmetric diffusion, $r_1 \neq r_2$ and for instance $K_1 > K_2$, the global carrying capacity reads as follows:

$$K_{Heterogeneous,Sym} = \frac{2K_1 K_2 (r_1 + r_2)}{(K_2 r_1 + K_1 r_2)} \tag{10}$$

It is easy to check that the total population in the homogeneous case can never be exceeded by that of the heterogeneous case, i.e. $K_{Heterogeneous,Sym} < K_{Homogeneous,Sym}$, equivalent to $K_2 < K_1$, see also Wang and DeAngelis (2019).

In order to have a total carrying capacity greater than the sum of isolated local ones, we need heterogeneity and asymmetric diffusion. As an example, let us choose $K_1 = K_2 = 50$, $r_1 = 10$, $r_2 = 1$ and $u = \frac{1}{3}$ then, $K = 128.57 > 100$. Therefore, the total equilibrium fish biomass of the system of connected logistic patches can be greater than the sum of equilibrium biomass of isolated patches. In other words, we have $B^* = K > K_1 + K_2$, see Poggiale et al. (2005), Freedman and Waltman (1977) and Arditi et al. (2015) for a complete analysis of the two-patch model.

2.2. With harvesting

We continue with a new part in which we assume that the fish population is exploited with a correspondingly identical rate in each of the two sites. We will now ask ourselves if the total productivity of the fishery by connecting the two fishing systems can be improved compared to the case of disconnected sites.

We still consider a system of two patches connected by fast migrations where fish sub-populations grow logistically, see Fig. 1. We still assume that the exchanges between the sites are fast in comparison to local growth and fishing. The only change we consider is to assume that the fish population is harvested in both sites. The complete model reads as follows:

$$\frac{dB_1}{d\tau} = m_2 B_2 - m_1 B_1 + \epsilon\left(r_1 B_1 (1 - \frac{B_1}{K_1}) - qEB_1\right) \tag{11}$$
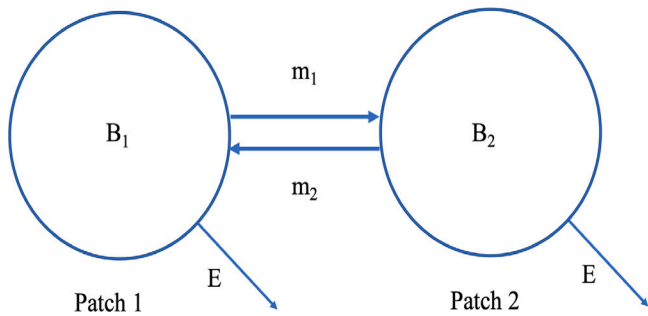
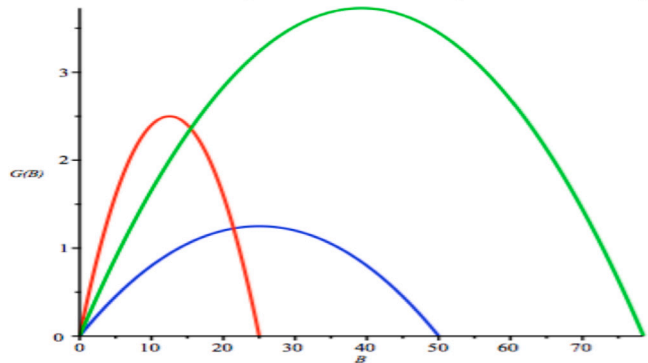**Fig. 1.** System of two connected patches with fast migration and harvesting.

Fig. 2. Logistic growth functions of patch 1 (blue), patch 2 (red) and aggregated system (green). Parameter set : $r_1 = 0.1$, $r_2 = 0.4$, $K_1 = 50$, $K_2 = 25$, $u = 0.7$, $r = r_1 u + r_2 (1 - u) = 0.19$ and $K = \frac{K_1 K_2 (r_1 u + r_2 (1-u))}{(K_2 r_1 u^2 + K_1 r_2 (1-u)^2)} = 78.51$.

$$\frac{dB_2}{d\tau} = m_1 B_1 - m_2 B_2 + \epsilon \left(r_2 B_2 (1 - \frac{B_2}{K_2}) - qEB_2 \right) \tag{12}$$

We assume a Schaefer catch on each patch i, (Schaefer, 1957), i.e. qEB_i, $i = 1, 2$, where E is the fishing effort and q is the catchability. For sake of simplicity we set $q = 1$ in the next parts. In the case of constant migrations, using the same reduction method as before, we obtain an aggregated model which reads as follows:

$$\frac{dB}{dt} = rB(1 - \frac{B}{K}) - EB \tag{13}$$

where r and K are the same as in the previous sub-section without fishing. In that case, the population equilibrium becomes $B^* = K(1 - \frac{E}{r})$ which is positive and stable when $E < r$. The maximum sustainable yield (MSY) for connected patches is obtained when $E = E^*_{MSY} = \frac{r}{2}$. In that case, the Maximum Sustainable Yield reads $Y^* = \frac{rK}{4}$, (Clark, 1990; Murray, 2002), see also for more details Appendix A.

On the other hand, for isolated patches (without migrations), we choose respectively $E_1 = \frac{r_1}{2}$ (resp. $E_2 = \frac{r_2}{2}$) for the fishing effort in patch 1, resp. 2. Then, the total Maximum Sustainable Yields are respectively $\frac{r_1 K_1}{4}$ and $\frac{r_2 K_2}{4}$ in each isolated patch. Now, we are going to compare at (MSY) the yield for the aggregated system to the sum of yields for isolated patches. We are going to show that :

$$\frac{rK}{4} \leq \frac{r_1 K_1}{4} + \frac{r_2 K_2}{4} \tag{14}$$

Indeed, substituting the expressions of the global growth rate $r = r_1 u + (1 - u) r_2$ and of the global carrying capacity $K = \frac{K_1 K_2 (r_1 u + r_2 (1-u))}{(r_1 u^2 + r_2 (1-u)^2)}$ of the aggregated model in the previous inequality, it comes:

$$\frac{(r_1 u + r_2 (1 - u))^2 K_1 K_2}{r_1 K_2 u^2 + r_2 K_1 (1 - u)^2} \leq r_1 K_1 + r_2 K_2 \tag{15}$$

For any $0 < u < 1$, after simplification, the inequality becomes $(K_1 (1 - u) - K_2 u)^2 > 0$ which is always verified. Therefore, while it

is possible to have a global equilibrium for connected patches greater than the sum of the carrying capacities for isolated sites, i.e. $B^* > K_1 + K_2$, it is impossible to have the maximum sustainable yield (MSY) for connected sites greater than the sum of yields at MSY for isolated patches. Fig. 2 shows logistic growth functions $(G(B))$ for patch 1, patch 2 and the aggregated model. These growth functions are negative parabola intersecting the horizontal axis at 0 and at the corresponding carrying capacity. At equilibrium, we check $rB^*(1 - \frac{B^*}{K}) = EB^*$ for any growth function. For each growth curve the MSY is found when B is at half the carrying capacity. In other words, the catch at MSY equals the value of the growth function at half of the carrying capacity. It thus corresponds to the maximum of each growth function between the origin and the carrying capacity. Fig. 2 shows just an example with $r_2 > r_1$ and $K_2 < K_1$ and $K > K_1 + K_2$ for $u = 0.7$. The slope of each logistic growth function is equal to the growth rate at the origin. We know that $r_1 < r < r_2$, the growth function of the aggregated model must be between the two growth curves of each patch at least when B is close to zero. Fig. 2 shows an example where even if $K > K_1 + K_2$, $\frac{rK}{4} = 3.73$ does not exceed $\frac{r_1 K_1}{4} + \frac{r_2 K_2}{4} = 3.75$. For $u = 1$, the green curve of the aggregated model is the same as the blue curve and for $u = 0$ it is similar to the red one. For any u in between, the curve of the aggregated system lies between the other two. Intuitively, because the growth curve of the aggregated model is mostly framed by the two growth curves of each patch, the catch of the fishery of the two coupled sites must always be less (or equal) than the sum of the catches of the two isolated sites. In other words, if the global carrying capacity can be greater than the sum of the local carrying capacity, the overall growth rate is always lower than the greater of the local growth rates, which limits the overall catch which can never exceed the sum of local catches.

This result is negative but it shows that in the simplest case of a single fish population exploited on two sites, it is impossible to increase the total productivity of the fishery by connecting the two sites between them. We will now show in the next section that this becomes possible when we consider a fish prey–predator system from which the predator is captured.

3. The two-patch prey–predator model with Lotka–Volterra functional response and constant fast migrations

3.1. Presentation and reduction of the two-patch prey–predator model

We consider a prey–predator fish community in a two-patch environment. The movements between patches are still described by constant rates and fast in comparison to local dynamics. Let us consider the following model:

$$\frac{dB_1}{d\tau} = m_2 B_2 - m_1 B_1 + \epsilon r_1 B_1 (1 - \frac{B_1}{K_1}) - \epsilon a_1 B_1 P_1 \tag{16}$$

$$\frac{dB_2}{d\tau} = m_1 B_1 - m_2 B_2 + \epsilon r_2 B_2 (1 - \frac{B_2}{K_2}) - \epsilon a_2 B_2 P_2 \tag{17}$$

$$\frac{dP_1}{d\tau} = k_2 P_2 - k_1 P_1 + \epsilon \left(e a_1 B_1 P_1 - d P_1 - E P_1 \right) \tag{18}$$

$$\frac{dP_2}{d\tau} = k_1 P_1 - k_2 P_2 + \epsilon \left(e a_2 B_2 P_2 - d P_2 - E P_2 \right) \tag{19}$$

where B_i and P_i are respectively fish prey and predator biomass on patch i, $i = 1, 2$. Parameters r_i and K_i represent the fish prey intrinsic growth rate and carrying capacity on patch i. Fig. 3 shows the system of connected patches. The fish prey and predator can move in both sites.

The fish predator catches the fish prey in both patches. a_i is the predation parameter in patch i. e is the conversion parameter of prey biomass into predator biomass. d is the predator mortality rate. The predator is harvested in both sites at a constant fishing effort E. Prey and predator are assumed to move fast with respect to local growth and predation. Prey (respectively) predator leave patch 1 to go to patch 2
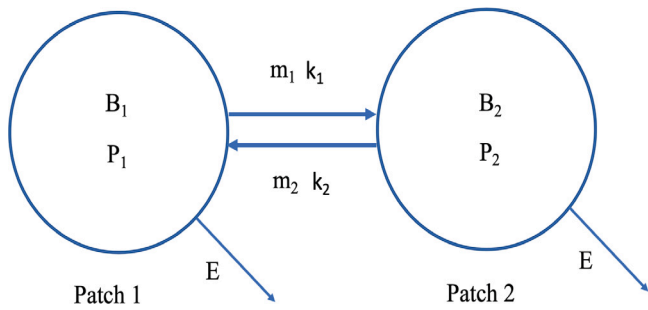
Fig. 3. System of two connected patches with fast migration and harvesting.

at the constant rate m_1, resp. k_1. Prey (respectively) predator return to patch 1 leaving patch 2 at constant rate m_2, resp. k_2. Time scales are still included in the model by using the fast time variable τ together with the positive dimensionless parameter $\epsilon \ll 1$.

The fast system is obtained by setting $\epsilon = 0$ in the complete system. In our case, the fast equilibrium for the fish prey is given by:

$$B_1^* = uB = \frac{m_2}{m_1 + m_2}B \tag{20}$$

$$B_2^* = (1-u)B = \frac{m_1}{m_1 + m_2}B \tag{21}$$

Where u represents the constant proportion of fish prey biomass in patch 1 and $(1-u)$ in patch 2 at the fast equilibrium.

In the same way, the fast equilibrium for the fish predator is given by:

$$P_1^* = vP = \frac{k_2}{k_1 + k_2}P \tag{22}$$

$$P_2^* = (1-v)P = \frac{k_1}{k_1 + k_2}P \tag{23}$$

Where v represents the constant proportion of predator biomass in patch 1 and $(1-v)$ in patch 2 at the fast equilibrium.

A reduced model is obtained by substituting the fast stable equilibrium into the complete system. Adding two by two equations for fish prey and predator biomass and by using slow time, we get the following aggregated model governing the total fish prey biomass $B = B_1 + B_2$ and fish predator $P = P_1 + P_2$ at the slow time which is also valid when it is structurally stable and for small enough value of ϵ:

$$\frac{dB}{dt} = rB(1 - \frac{B}{K}) - aBP + O(\epsilon) \tag{24}$$

$$\frac{dP}{dt} = eaBP - dP - EP + O(\epsilon) \tag{25}$$

The overall fish prey growth rate of the reduced model still reads:

$$r = r_1 u + (1-u)r_2 \tag{26}$$

as well as the overall prey carrying capacity:

$$\frac{r}{K} = \frac{r_1 u^2}{K_1} + \frac{r_2(1-u)^2}{K_2} \tag{27}$$

We also get an overall predation parameter a:

$$a = a_1 uv + a_2(1-u)(1-v) \tag{28}$$

Assuming that $d + E < eaK$, there exists a positive interior equilibrium. In the long term, B tends to B^* which reads:

$$B^* = \frac{d+E}{eau} \tag{29}$$

and P tends to P^*:

$$P^* = \frac{r}{a}(1 - \frac{d+E}{eaK}) \tag{30}$$

When the equilibrium (B^*, P^*) is positive, it is globally asymptotically stable in the positive quadrant.

Fig. 4 shows a comparison of the solutions of the complete (red) and aggregated (blue) models for $\epsilon = 0.1$. (Left) Upper solutions correspond to the total fish prey biomass simulated using the complete model (red) and the reduced aggregated model (blue), lower solutions to the total fish predator biomass. It shows that the solutions of both models remain very close when parameter ϵ is small enough, i.e. 0.1. The right figure shows the phase portrait still comparing the complete (red) and aggregated (blue) models for $\epsilon = 0.1$.

The calculation of the total catch at equilibrium is recalled in Appendix A. For the system of two coupled patches, the total catch is a function of the fishing effort as follows:

$$Y^*(E) = EP^* = \frac{rE}{a}(1 - \frac{(d+E)}{eaK}) \tag{31}$$

as well as for isolated patch 1:

$$Y_1^*(E) = EP^* = \frac{r_1 E}{a_1}(1 - \frac{(d+E)}{ea_1 K_1}) \tag{32}$$

and isolated patch 2:

$$Y_2^*(E) = EP^* = \frac{r_2 E}{a_2}(1 - \frac{(d+E)}{ea_2 K_2}) \tag{33}$$

Now, we consider the Maximum Sustainable Yield (MSY) associated with the fishing effort which maximizes the catch, see appendix. Let Y_{MSY}^* be the maximum yield for the system of the two connected patches by fast migrations which is given by the next expression:

$$Y_{MSY}^* = \frac{r}{4ea^2 K}(eaK - d)^2 \tag{34}$$

and it must be compared to the maximum yields at MSY for patch 1:

$$Y_{MSY1}^* = \frac{r_1}{4ea_1^2 K_1}(ea_1 K_1 - d)^2 \tag{35}$$

and patch 2:

$$Y_{MSY2}^* = \frac{r_2}{4ea_2^2 K_2}(ea_2 K_2 - d)^2 \tag{36}$$

3.2. Comparison at MSY of the global yield in case of connected sites with the sum of yields of isolated sites in the Lotka–Volterra model with type I functional response

Let us see if the maximum yield for connected patches can be greater than the sum of yields associated with single isolated patches. In other words, let us check if:

$$Y_{MSY}^* > Y_{MSY1}^* + Y_{MSY2}^* \tag{37}$$

Let us define the Yield excess as follows:

$$\Delta Y_{MSY}^* = Y_{MSY}^* - (Y_{MSY1}^* + Y_{MSY2}^*) \tag{38}$$

We are now going to look for the conditions allowing to obtain a positive excess yield.

3.2.1. Homogeneous case

Let us consider the homogeneous case, i.e., $K_1 = K_2$, $r_1 = r_2$, $a_1 = a_2$. Furthermore, we assume that the predator distributes spatially like its prey, $v = u$. Parameters of the aggregated model are the following:

$$r = r_1 \tag{39}$$

$$a = a_1(u^2 + (1-u)^2) \tag{40}$$

$$K = \frac{K_1}{(u^2 + (1-u)^2)} \tag{41}$$

After substitution in ΔY_{MSY}^*, it comes:

$$\Delta Y_{MSY}^* = \frac{r_1(ea_1 K_1 - d)^2}{4ea_1^2 K_1}(\frac{1}{(u^2 + (1-u)^2)} - 2) \tag{42}$$
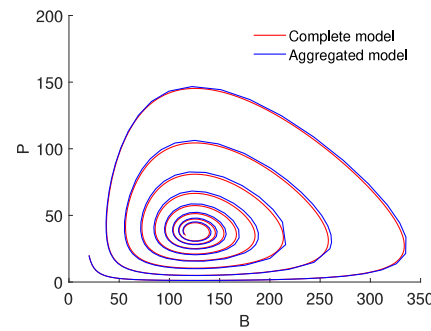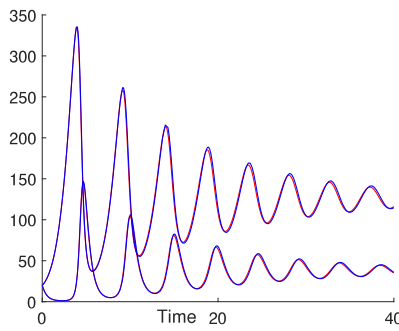
Fig. 4. Comparison of the solutions of the complete (red) and aggregated (blue) models for $\epsilon = 0.1$ with respect to fast time τ. (Left) time evolution of total prey (upper solutions) and total predator (lower solutions) biomass. (Right) phase portrait. Parameters values are $K_1 = 800$, $K_2 = 80$, $r_1 = 10$, $r_2 = 7.5$, $m_1 = 10$, $m_2 = 90$, $k_1 = 20$, $k_2 = 80$, $a_1 = 0.3$, $a_1 = 0.2$, $e = 0.8$, $E = 17.16$, $d = 5$, $v = 0.8$, and $u = 0.9$. Initial conditions are $B_1(0) = B_2(0) = P_1(0) = P_2(0) = 10$ for complete model and $B(0) = P(0) = 20$ for aggregated model.
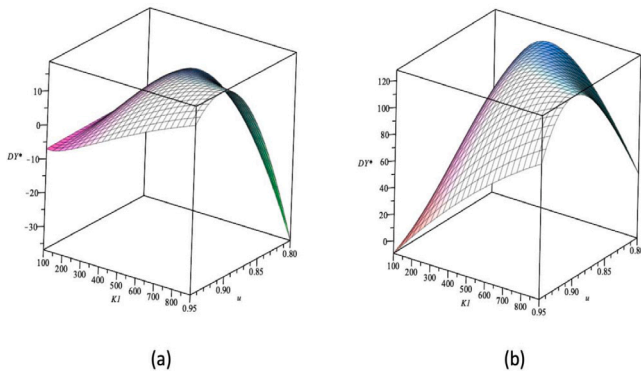

Fig. 5. Yield excess as a function of the proportion of prey in patch 1 and of the carrying capacity K_1 for prey in patch 1. (a) Almost homogeneous case : $K_2 = 100$, $r_1 = r_2 = 2$, $a_1 = a_2 = 0.2$, $v = 0.9$, $e = 0.8$ and $d = 10$. (b) Heterogeneous case : $K_2 = 100$, $r_1 = 2$, $r_2 = 8$, $a_1 = 0.8$, $a_2 = 0.2$, $v = 0.9$, $e = 0.8$ and $d = 10$.

Therefore, in order to have a positive excess yield, $\Delta Y^*_{MSY} > 0$, we would need to check:

$$g(u) = (u^2 + (1-u)^2) < \frac{1}{2} \tag{43}$$

As $0 < u < 1$, this is never possible. Indeed, $g(0) = g(1) = 1$. Furthermore, $g(u)$ has a minimum when $u = \frac{1}{2}$ and $g(\frac{1}{2}) = \frac{1}{2}$.

Therefore, for any similar spatial distribution of the prey and predator fish, symmetric or not, it is impossible to have a positive excess yield in the homogeneous case.

3.2.2. Heterogeneous case

Fig. 5(a) shows an almost homogeneous case where the two sites are similar, same growth rate r and same predation parameter a. Here we fix the proportion v of predators in zone 1 and we will vary the proportion of preys u. We assume that the predator is mainly located in patch 1, by choosing $v = 0.9$. As expected, when $K_1 = K_2 = 100$, the yield excess is negative. Then we break the homogeneity by increasing K_1 and we look at the effect of the prey proportion. The global maximum in this range of parameters (u, K_1) is about 20. Fig. 5(b) shows an heterogeneous case with respect to (a) where the growth rate r_2 is much larger in patch 2 and the predation parameter is much larger in patch 1 compared to the homogeneous case (a). The global maximum in this range of parameters (u, K_1) is much higher about 130. Site 2 has a high growth rate with few predators. As a result, it constitutes a productive site, a reservoir of preys which are little captured and migrate to site 1 where the predators are numerous and very efficient. This would explain the increase of the global productivity at MSY of the system of connected patches with respect to isolated patches. Therefore, we could interpret this result as a spillover effect

Table 1
Table of yields at MSY: Y^*_{MSY}, Y^*_{MSY1}, ΔY^*_{MSY}, $\%\Delta Y^*_{MSY}$ with respect to the proportion of prey in patch 1, with parameter set of the heterogeneous case : $K_1 = 900$, $K_2 = 100$, $r_1 = 2$, $r_2 = 8$, $a_1 = 0.8$, $a_2 = 0.2$, $v = 0.9$, $e = 0.8$ and $d = 10$.

u	Y^*_{MSY}	$Y^*_{MSY1} + Y^*_{MSY2}$	ΔY^*_{MSY}	$\%\Delta Y^*_{MSY}$
0.86	480	370	109	29.6%
0.88	494	370	124	33.4%
0.90	500	370	130	35.1%
0.92	496	370	125	33.9%
0.94	477	370	107	29.0%

of the prey reservoir. Fig. 5(b) shows that the global maximum in this range, $\Delta Y^*_{MSY}(u, K_1) \approx 130$, is obtained when the carrying capacity K_1 is the largest, i.e. $K_1 = 900$, and for a prey proportion at the ideal free distribution (IFD) (Bernstein et al., 1999), see Table 1. We define the percentage of yield excess as $\%\Delta Y^*_{MSY} = \frac{100\Delta Y^*_{MSY}}{(Y^*_{MSY1}+Y^*_{MSY2})}$ which equals 35.1% at the global maximum of Fig. 5(b). Table 1 shows that the maximum excess yield is obtained when the prey is at IFD, i.e. when $u = \frac{K_1}{K_1+K_2} = 0.9$.

A strong heterogeneity between the two patches with an asymmetric spatial distribution of the prey (to be at IFD) and of the predator, with $u = v$, favors the increase of the yield excess. In Appendix B, we show the following general condition to have a positive excess yield ΔY^*_{MSY} :

$$\frac{(\alpha u^2 + \beta(1-u)^2)}{\alpha(u^2 + \gamma(1-u)^2)}(ea_1\alpha K_1 \frac{(u+\beta(1-u))(u^2+\gamma(1-u)^2)}{(\alpha u^2 + \beta(1-u)^2)} - d)^2$$
$$> (ea_1 K_1 - d)^2 + \frac{\beta}{\gamma^2 \alpha}(e\gamma a_1 \alpha K_1 - d)^2 \tag{44}$$

where we consider a heterogeneous case characterized by dimensionless positive parameters of heterogeneity α, β and γ defined as follows:

$$K_2 = \alpha K_1 \tag{45}$$

$$r_2 = \beta r_1 \tag{46}$$

$$a_2 = \gamma a_1 \tag{47}$$

A very heterogeneous system means that α is small (respectively large) i.e. the carrying capacity of patch 2 is small (respectively large) compared to that of patch 1 and similarly for β and γ with respect to growth rates and predator efficiency. Furthermore, assuming a highly asymmetric distribution, for instance $u \ll 1$, it is shown in Appendix B that the previous formula becomes:

$$\frac{\beta}{\alpha\gamma}(ea_1\alpha\gamma K_1 \frac{(u+\beta(1-u))}{\beta} - d)^2 > (ea_1 K_1 - d)^2 + \frac{\beta}{\gamma^2\alpha}(e\gamma a_1\alpha K_1 - d)^2 \tag{48}$$

For example, choosing $u = 0.1$, $\beta = \alpha = 100$, then $\alpha = 0.01$ and the inequality is checked. Indeed, the right hand side is small of the order of $0.02(ea_1 K_1 - d)^2$ while the left hand side is of the order of $(ea_1 K_1 - d)^2$.
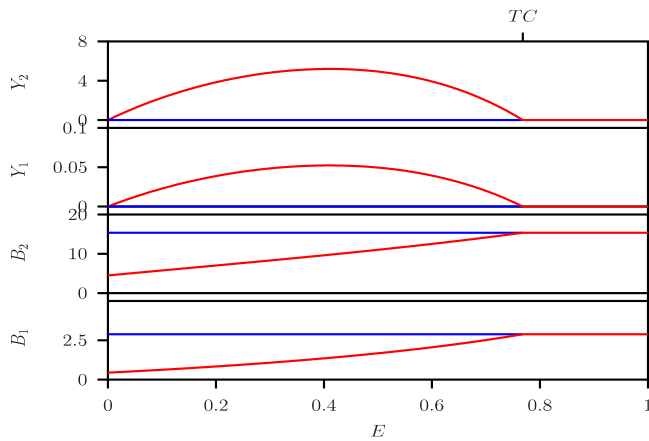
Fig. 6. Bifurcation analysis with respect to E where $K_1 = 75, K_2 = 15$ and $\varepsilon = 0.05$ for the complete system. The other fixed parameter values are: $D = 25$, $r_1 = 0.05$, $r_2 = 2.5$, $a = 2$, $e = 1.0$, $d = 0.3$ and $m_1 = 0.1, m_2 = 0.185$ and $k_1 = 0.02, k_2 = 0.98$. Top panels: yield $Y_1 = EP_1$ and $Y_2 = EP_2$, bottom panels B_1 and B_2. Red: stable equilibrium. Blue: unstable equilibrium values. Point TC denotes the transcritical.

Fig. 7. Catch at equilibrium with respect to E, with parameter set: $K_1 = 75$, $K_2 = 15$, $D = 25$, $r_1 = 0.05$, $r_2 = 2.5$, $a = 2$, $e = 1$, $d = 0.3$, $u = 0.65$ and $v = 0.98$.

Consequently, conditions of strong heterogeneity with an asymmetrical distribution make it possible to obtain a positive yield excess.

4. The 2-patch Holling type II predator–prey model with fast migrations

We consider a system of two fishing areas connected by migrations. We consider the prey–predator model with a Holling type II functional response at each patch. The prey and its predator can move from one fishing area to another. The complete model reads as follows:

$$\frac{dB_1}{d\tau} = m_2 B_2 - m_1 B_1 + \epsilon \left(r_1 B_1 \left(1 - \frac{B_1}{K_1}\right)\right) - \epsilon \left(\frac{aB_1 P_1}{B_1 + D}\right) \tag{49}$$

$$\frac{dB_2}{d\tau} = m_1 B_1 - m_2 B_2 + \epsilon \left(r_2 B_2 \left(1 - \frac{B_2}{K_2}\right)\right) - \epsilon \left(\frac{aB_2 P_2}{B_2 + D}\right) \tag{50}$$

$$\frac{dP_1}{d\tau} = k_2 P_2 - k_1 P_1 + \epsilon \left(\frac{eaB_1 P_1}{B_1 + D} - dP_1 - EP_1\right) \tag{51}$$

$$\frac{dP_2}{d\tau} = k_1 P_1 - k_2 P_2 + \epsilon \left(\frac{eaB_2 P_2}{B_2 + D} - dP_2 - EP_2\right) \tag{52}$$

We use the same notations as before. We assume the same predation parameters a and D in each patch. For instance, we assume that the prey handling time for the predator is the same in both patches.

The Fig. 6 shows the results for the numerical bifurcation analysis of the complete model Eqs. (49)–(52). This example is for the parameter set : $K_1 = 75$, $K_2 = 15$, $D = 25$, $r_1 = 0.05$, $r_2 = 2.5$, $a = 2$, $e = 1.0$, $d = 0.3$, $m_1 = 0.1$, $m_2 = 0.185$ and $k_1 = 0.02$, $k_2 = 0.98$ with $\varepsilon = 0.05$. Below the transcritical bifurcation TC the predator is extinct. Above TC there exists a stable interior equilibrium.

After reduction, the aggregated model reads as follows:

$$\frac{dB}{dt} = rB\left(1 - \frac{B}{K}\right) - \frac{auvBP}{uB + D} - \frac{a(1-u)(1-v)BP}{(1-u)B + D} \tag{53}$$

$$\frac{dP}{dt} = \frac{eauvBP}{uB + D} + \frac{ea(1-u)(1-v)BP}{(1-u)B + D} - dP - EP \tag{54}$$

We still note u and v as the prey and predator proportions in patch 1 at the fast equilibrium. Hence the fast migration equilibrium equations Eqs. (20), (23) also hold now for all times. The expressions for the prey populations r, Eq. (6), and K, Eq. (8), are the same as in previous cases. Adding the two equations for the prey Eq. (49)–(50) and predator Eqs. (51)–(52) gives the aggregated model Eqs. (53), (54). This shows that the aggregated four dimensional system and the two dimensional system are equivalent where the analysis of the two dimensional system
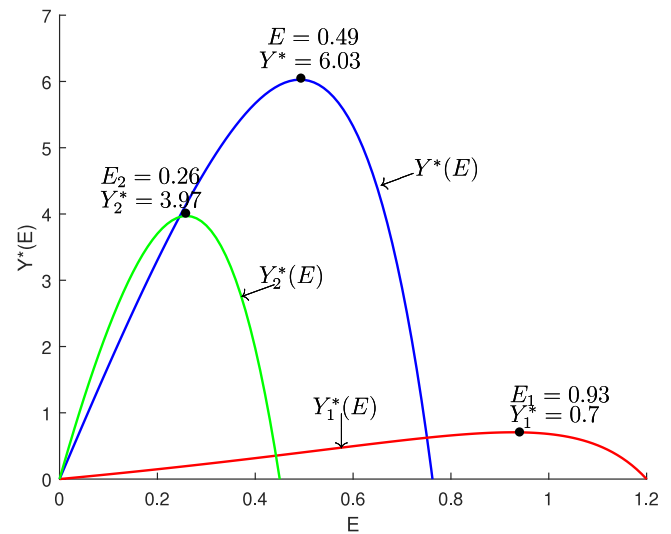
is simpler. The interior equilibrium equation for the prey population Eq. (53) gives the explicit expression for the predator equilibrium P^* and substitution in Eq. (54) an implicit expression for the prey B^*.

Note also that $\frac{eauvBP}{uB+D} + \frac{ea(1-u)(1-v)BP}{(1-u)B+D} - dP - EP < (ea-d-E)P$ because $\frac{uB}{uB+D} < 1$ and $\frac{(1-u)B}{(1-u)B+D} < 1$. As a consequence, $\frac{dP}{dt} < (ea - d - E)P$ and we assume that $ea > d + E$ to have predator persistence.

The interior equilibrium (B^*, P^*) where

$$P^* = \frac{re}{d + E} B^* \left(1 - \frac{B^*}{K}\right) \tag{55}$$

which is positive when $B^* < K$ where B^* is the positive root of the equation

$$F(B) = \alpha_1 B^2 + \alpha_2 B - \alpha_3 = 0 \tag{56}$$

where the coefficients are

$\alpha_1 = (ea - (d + E))u(1 - u)$,
$\alpha_2 = eaD(uv + (1 - u)(1 - v)) - D(d + E)$,
$\alpha_3 = (d + E)D^2$.

As by hypothesis $\alpha_1 > 0$, by Descartes' rule of signs, it follows that there is one positive real root of (56) given by

$$B^* = \frac{-eaD(uv + (1-u)(1-v)) + D(d+E) + \sqrt{\Delta}}{2(ea - (d+E))u(1-u)} \tag{57}$$

where the discriminant Δ of the polynomial F is given by

$$\Delta = [eaD(uv + (1-u)(1-v)) - D(d+E)]^2 + 4(d+E)D^2(ea - (d+E))u(1-u)$$

The yield $Y^*(E) = EP^*$ reads as follows:

$$Y^*(E) = EP^* = re\frac{E}{d+E} B^* \left(1 - \frac{B^*}{K}\right) \tag{58}$$

We show an example with the parameter set : $K_1 = 75$, $K_2 = 15$, $D = 25$, $r_1 = 0.05$, $r_2 = 2.5$, $a = 2$, $e = 1$, $d = 0.3$, $u = 0.65$ and $v = 0.99$. Fig. 7 shows the graphs of the catch of connected sites and isolated sites as a function of the fishing effort E. Each curve has a maximum corresponding to the MSY. It is good to note that for the value of the fishing effort at MSY, $E = 0.49$, for the complete system of connected sites, the bifurcation diagram of Fig. 6 predicts a stable equilibrium. This result is in agreement with Fig. 8 showing the solutions of the reduced model with also a stable equilibrium. Simulations, not shown here, show that for each isolated site there is also a stable equilibrium. This allows us to calculate the optimal catch at MSY of the system of connected sites and compare with the optimal ones of isolated sites. Fig. 7 shows that for this example, there is a positive excess yield equal
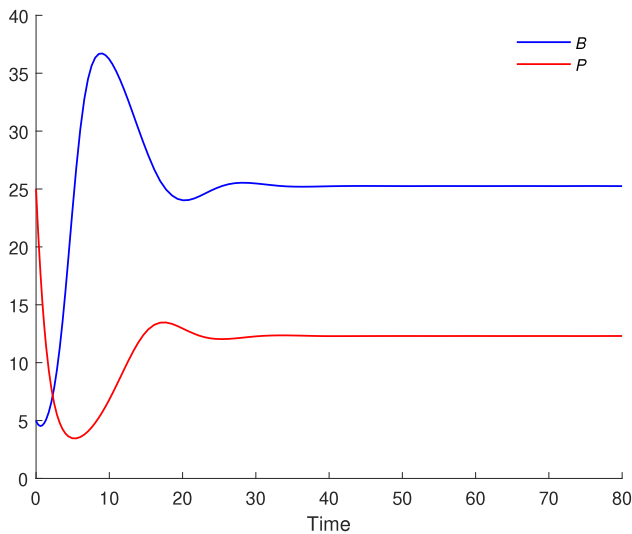
Fig. 8. Solutions of the aggregated model with respect to time, with parameter set: $K_1 = 75$, $K_2 = 15$, $D = 25$, $r_1 = 0.05$, $r_2 = 2.5$, $a = 2$, $e = 1$, $d = 0.3$, $u = 0.65$, $v = 0.99$ and $E = 0.49$. Initial condition is $B(0) = 5$, $P(0) = 25$.

to $\Delta Y^*_{MSY} = 1.36$ with respect to $Y^*_{MSY1} + Y^*_{MSY2} = 4.67$, i.e. about %29 increase.

The type of ecosystem control remains a central question in theoretical ecology, (Leroux and Loreau, 2015). If the prey and predators do not move (or little), the predator will control the survival or extinction of the prey at each site with a top-down type of control. However, in our model, not only the predator but also its prey are free to move between the two sites. The preys can thus be distributed to optimize their overall growth and productivity by adopting the IFD. The fast movement of the prey is in a way a bottom-up control strategy. It seems that the loss of top-down control results in the prey increasing its productivity, which favors the predator and in turn increases its capture and the yield excess at the MSY.

5. Effects of connectivity of fishing sites on the total productivity of the fishery

We will now study the effect of the connection of two fishing sites by comparing the total catch at MSY of the coupled sites with that of the two isolated sites for two suggested application examples.

5.1. The case of a predator–prey fish community with type I functional response

Let us consider the predator–prey system of tuna and sardinella in West Africa, (Thiaw et al., 2017). Tuna live offshore, a huge site, but with less food and sardinella live on the continental shelf which is a smaller area, but very rich in food for sardinella, such as plankton. Tuna eat sardinella and sardinella eat plankton. Plankton is mainly on the continental shelf. Tuna are hampered by plankton (lack of visibility) so they stay most of time offshore and come on continental shelf to predate because sardinella is abundant. Thus in our example, the prey fish could be sardinella and the predator tuna. Fishing site 1 corresponds to the coastal zone, or continental shelf, and fishing site 2 to the high seas zone, or offshore. Sardinella abundance is correlated to coastal upwelling index, (Thiaw et al., 2017). When the upwelling is high, there are significant amounts of nutrients on the coast that are food for plankton. This allows high plankton density which is the food of small fish. For the sake of simplicity, we assume that the density of plankton is constant in both areas. It can be considered that the carrying capacity depends on the concentration of plankton in each zone. Plankton is more abundant in the coastal zone. In reality, sardinella is also
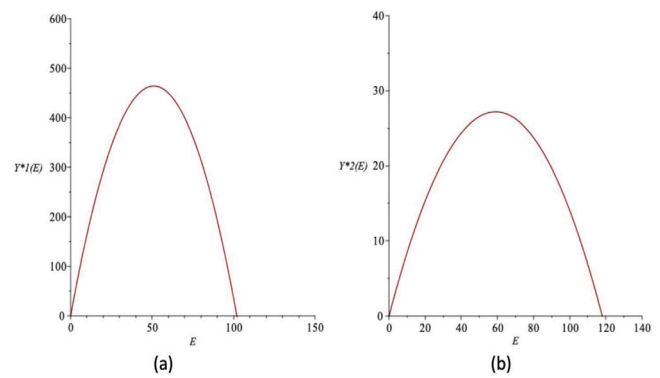

Fig. 9. Catch at equilibrium $Y^*_1(E)$ for fishing site 1 (a) and catch $Y^*_2(E)$ for fishing site 2 (b) as a function of the fishing effort E. Parameters values are $K_1 = 700$, $K_2 = 80$, $r_1 = 4$, $r_2 = 2$, $a_1 = 0.2$, $a_2 = 2$, $u = 0.85$, $v = 0.15$, $e = 0.8$ and $d = 10$.
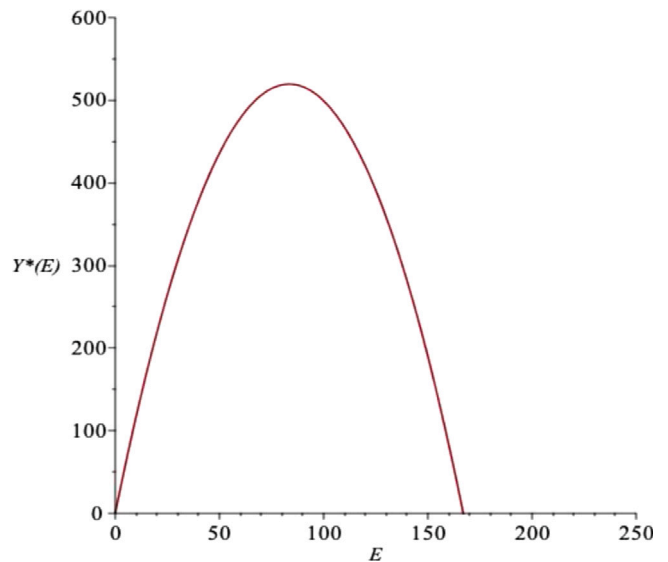

Fig. 10. Catch at equilibrium $Y^*(E)$ for the system of the two connected fishing sites. Parameters values are $K_1 = 700$, $K_2 = 80$, $r_1 = 4$, $r_2 = 2$, $a_1 = 0.2$, $a_2 = 2$, $u = 0.85$, $v = 0.15$, $e = 0.8$ and $d = 10$.

caught and not just tuna. In addition, there are different industrial and artisanal fishing fleets that exploit both species. The tuna does not only eat sardinella but also other small fish as well as squid. We therefore do not have the ambition to describe the tuna/sardinella prey–predator system with a too simple model. At this stage, we propose a potential example of application with values of parameters which respect the conditions of heterogeneity and predation pressure in the two zones such as in the example of the tuna/sardinella system.

Thus, in our example, we set $K_1 = 700$ in coastal area and $K_2 = 80$ offshore. We also assume that the growth of sardinella is better in the coastal area, $r_1 = 4$ and $r_2 = 2$. Tunas are more effective at catching sardinella in the open sea rather than in coastal area, so we set $a_1 = 0.2$ and $a_2 = 2$. We also choose $e = 0.8$ and similar predator mortality in the two zones, $d = 10$. Sardinellas spend a large part of their time in coastal areas so we assumed that $u = 0.85$. The tunas stay most of the time on the high seas and make forays into coastal areas and we have chosen $v = 0.15$.

Fig. 9 shows equilibrium catches in the two "isolated" fishing zones as a function of the fishing effort. Each of them shows a maximum corresponding to the MSY. The maximum catch in the first fishing site is equal to $Y^*_{MSY1} = 464$. For the second one, the optimal catch is equal to $Y^*_{MSY2} = 27$. Fig. 10 shows that the equilibrium catch in the system of
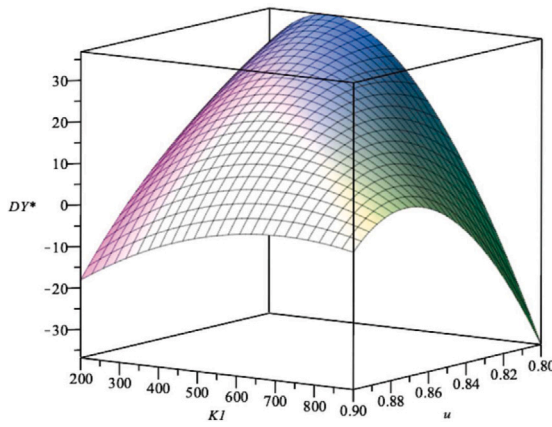
Fig. 11. Yield excess DY^*_{MSY} as a function of prey fish proportion u and carrying capacity K_1 in site 1. Parameters values are $K_2 = 80$, $r_1 = 4$, $r_2 = 2$, $a_1 = 0.2$, $a_2 = 2$, $v = 0.15$, $e = 0.8$ and $d = 10$.

connected fishing sites as a function of the fishing effort. The curve also shows a maximum corresponding to the MSY. The maximum catch in the system of connected fishing areas is equal to $Y^*_{MSY} = 520$. This value of the total catch of the fishery at MSY is obtained when the two fishing sites are connected by fish migrations. It is greater than the sum of the maximum catches of the two fishing sites if they would be isolated and exploited separately. The excess productivity of the fishery is equal to $\Delta Y^*_{MSY} = 29$ which corresponds to a small but positive percentage gain at 5.9%.

On another hand, artificial reefs are known to have an effect on fish productivity. Therefore, the establishment of artificial reefs in coastal areas makes it possible to increase the carrying capacity of small fish like sardinella. It seems possible to seek to fix the carrying capacity of the coastal zone in order to optimize the excess yield. Fig. 11 shows the yield excess as a function of prey fish proportion u and carrying capacity K_1 in fishing zone 1. It shows that for a fixed carrying capacity K_1, there is a maximum when the prey distributes at IFD. It also shows that at fixed prey proportion in site 1, there is a value of the carrying capacity K_1 that maximizes the excess yield. Thus, we could think of installing artificial reefs in coastal areas to set the carrying capacity at some optimal value leading to a better excess yield.

Another important aspect concerns the installation of marine protected areas (MPA). In the complete Lotka–Volterra model of connected sites with 4 equations, it is possible to consider different fishing effort E_1 and E_2 on each site. In the aggregated model reduced to 2 equations, it is easy to check that nothing will be changed except the overall fishing effort which will be written:

$$E = E_1 v + E_2(1 - v) \tag{59}$$

In this case, there are two control variables E_1 and E_2 and finding the MSY is a more difficult problem not addressed in this work. However, in the case of an MPA, the problem is simplified to a single variable, the fishing effort of the area which is not MPA. If, for example, zone 2 is MPA, you have to choose the global effort $E^*_{MSY} = \frac{(eaK-d)}{2}$ to be at MSY. In this case, we will have to fish more in fishing site 1 because we have the following relation:

$$E_1 v = \frac{(eaK - d)}{2}, \quad v < 1 \tag{60}$$

More fishing must be done in the fishing area to reach the MSY to compensate for the loss of catch in the protected area.

The study of the effects of marine reserves in fishery modeling has received a great deal of attention, (Hannesson; Grafton et al., 2005; Greenville and MacAulay, 2006) for a two patch model with two species and protected areas. Most models focus on the effect on the total

population as well as on the resulting increase in fishermen's income in a stable environment or with ecological uncertainty. However, in our study, we are looking for the conditions of heterogeneity and asymmetric diffusion that make it possible to obtain an overall productivity of the fishery higher than that of isolated fisheries at MSY.

5.2. The case of a predator–prey fish community with Holling type II functional response

We now study a predator–prey model with a Holling type II functional response. Thus, we still consider a prey–predator community in a two-patch environment with two marine zones, one with a high carrying capacity and the other with a smaller carrying capacity for the prey. In this new example, the first area is a fishing area where the prey and its predator can stay. We suppose that the second zone is a mangrove. The mangrove forms a shelter for juvenile fish and small prey fish to predators. Predators have great difficulty in catching prey in the mangrove because of the turbidity of the water which prevents them from detecting the prey. It is also usual to consider that mangroves allow fish to grow faster because they spend more time feeding than escaping their predator. Some predatory fish may venture into the mangroves but they do not stay there for long because they capture little prey fish. Larger carnivorous fish do not venture deep inside the mangrove, (Rönnbäck et al., 1999). We will consider an example where prey is abundant in the common area. Consequently and for the sake of simplicity we will further assume that the predator is a large one and remains only in the fishing zone. Thus, the predator does not move and stays in patch 1 where it is harvested at constant rate E. In this example, we assume a Holling type II functional response. The complete model reads as follows:

$$\frac{dB_1}{d\tau} = m_2 B_2 - m_1 B_1 + \epsilon\left(r_1 B_1(1 - \frac{B_1}{K_1})\right) - \epsilon\left(\frac{a B_1 P}{B_1 + D}\right) \tag{61}$$

$$\frac{dB_2}{d\tau} = m_1 B_1 - m_2 B_2 + \epsilon\left(r_2 B_2(1 - \frac{B_2}{K_2})\right) \tag{62}$$

$$\frac{dP}{d\tau} = \epsilon\left(\frac{ea B_1 P}{B_1 + D} - dP - EP\right) \tag{63}$$

We use the same notations as in the previous models. a is the predation parameter in patch 1. $D > 0$ is another predation parameter associated with the handling time. In reality, the mangrove is an area where juvenile fish mainly thrive. It would therefore be necessary to develop a more complex model with age or size classes of prey fish. Here we consider a simple example with an unstructured prey population. In this example, site 1 is a fishing area and site 2 is the mangrove. We assume that the prey fish are abundant in the fishing area, $K_1 = 75$ and less in the mangrove $K_2 = 5$. We also assume that prey fish growth rate is higher in the mangrove, $r_1 = 0.5$ and $r_2 = 2.5$. Other parameters are the following, $a = 2$, $D = 5$, $e = 0.5$, $d = 0.5$ and $u = 0.95$.

The Fig. 12 shows the results for the bifurcation analysis of the three dimensional complete model with prey refuge (61)–(63) with parameter set: $K_1 = 75$, $K_2 = 5$, $D = 5$, $r1 = 0.5$, $r2 = 2.5$, $a = 2$, $e = 0.5$, $d = 0.5$ and $m_1 = 0.05$ and $m_2 = 0.95$. With respect to E, above the transcritical bifurcation TC the predator is extinct. Between TC and the Hopf bifurcation H the equilibrium is stable and below H unstable with stable limit cycles. These results indicate that for a large region $E < 0.3$ the system can collapse due to stochastic effects (Rosenzweig, 1971).

After reduction, the aggregated model reads as follows:

$$\frac{dB}{dt} = rB(1 - \frac{B}{K}) - \frac{auBP}{uB + D} \tag{64}$$

$$\frac{dP}{dt} = \frac{eauBP}{uB + D} - dP - EP \tag{65}$$

This reduced model is a classical Rosenzweig–MacArthur model (Rosenzweig and MacArthur, 1963), where u is the proportion of fish
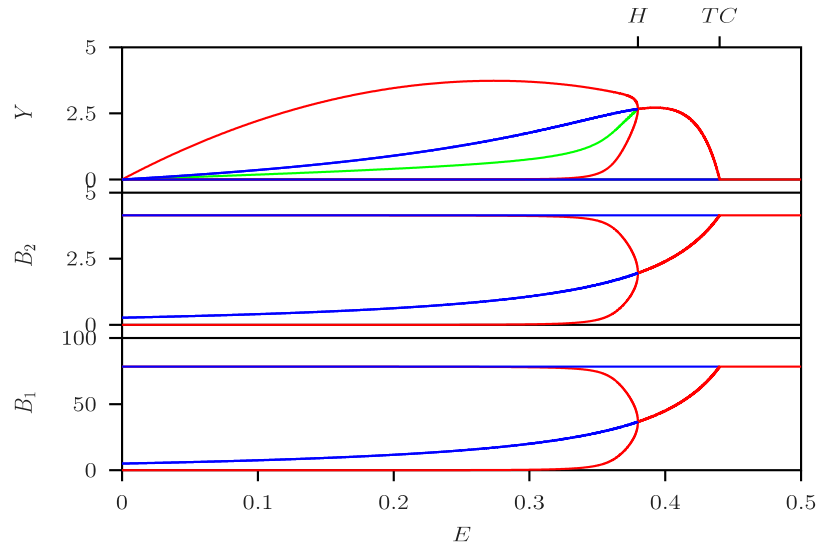
Fig. 12. Bifurcation analysis with respect to E where $K_1 = 75, K_2 = 5$ and $\varepsilon = 0.01$ for the complete model with prey refuge. The other fixed parameter values are: $D = 5$, $r_1 = 0.5$, $r_2 = 2.5$, $a = 2$, $e = 0.5$, $d = 0.5$ and $m_1 = 0.05, m_2 = 0.95$, that is $u = 0.95$. Top panel: yield $Y = EP$, middle panel B_2 and lower panel B_2. Red: stable equilibrium or maximum and minimum limit cycle values. Blue: unstable equilibrium values. Green: mean yield value for the limit cycle. Threshold point TC denotes the transcritical and point H the Hopf bifurcation.
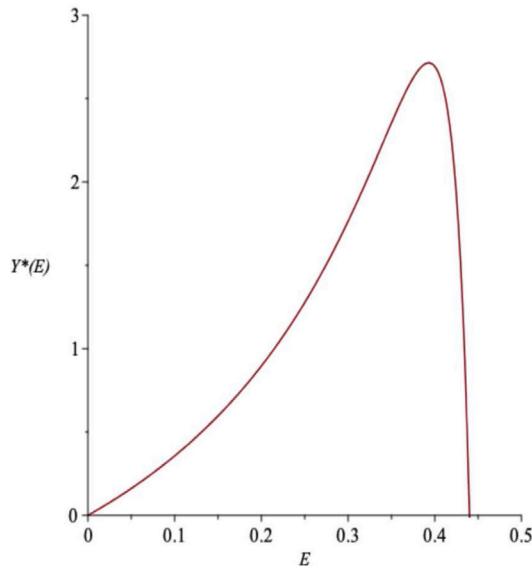

Fig. 13. Function $Y^*(E)$ with respect to E, with parameter set: $K_1 = 75$, $K_2 = 5$, $D = 5$, $r1 = 0.5$, $r2 = 2.5$, $a = 2$, $e = 0.5$, $d = 0.5$ and $u = 0.95$.
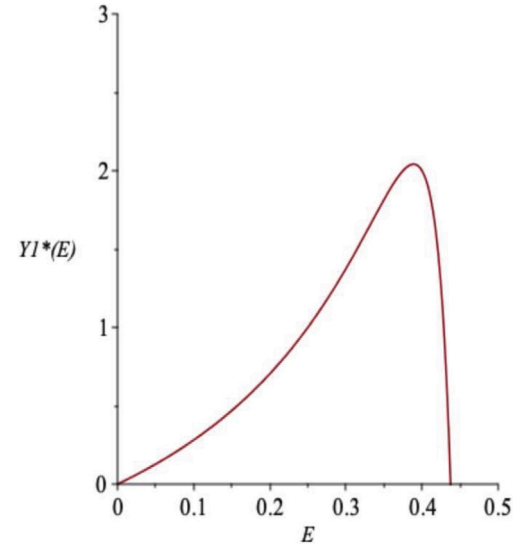

Fig. 14. Function $Y_1^*(E)$ with respect to E for isolated patch 1, with parameter set from Fig. 13.

prey in patch 1 at the fast equilibrium. r and K are defined as in the previous cases. The interior equilibrium reads:

$$B^* = \frac{(d+E)D}{u(ea - (d+E))} \tag{66}$$

which is positive when $E < ea - d$ and P^*:

$$P^* = (\frac{rDe}{u(ea-(d+E))})(1 - \frac{(d+E)D}{uK(ea-(d+E))}) \tag{67}$$

The equilibrium yield $Y^*(E) = EP^*$ reads as follows:

$$Y^*(E) = \frac{rDeE}{u(ea-(d+E))}(1 - \frac{(d+E)D}{uK(ea-(d+E))}) \tag{68}$$

The yield for isolated patch 1 reads:

$$Y_1^*(E) = \frac{r_1 DeE}{(ea-(d+E))}(1 - \frac{(d+E)D}{K_1(ea-(d+E))}) \tag{69}$$

Now let us look for the fishing effort that maximizes the total catch of the two connected fishing sites. This fishing effort corresponds to a zero of the derivative of the total catch, i.e. $\frac{dY^*(E)}{dE} = 0$. The calculation shows that there is a maximum of the total catch for the following value of the fishing effort corresponding to the MSY:

$$E_{MSY}^* = \frac{(ea-d)((ea-d)uK - dD)}{(ea-d)uK + (2ea-d)D} \tag{70}$$

similarly for isolated patch 1:

$$E_{1MSY}^* = \frac{(ea-d)((ea-d)K_1 - dD)}{(ea-d)K_1 + (2ea-d)D} \tag{71}$$

The catches at MSY are simply calculated as follows: $Y_{MSY}^* = Y^*(E_{MSY}^*)$ and $Y_{1MSY}^* = Y^*(E_{1MSY}^*)$.

In our example, $K_1 = 75$, $K_2 = 5$, $D = 5$, $r_1 = 0.5$, $r_2 = 2.5$, $a = 2$, $e = 0.5$, $d = 0.5$ with $u = 0.95$. We find the growth rate $r = 0.6$, Eq. (6), and the carrying capacity $K = 82.56$, Eq. (8). We have seen that for the system of the two connected marine zones by prey migration, there

Table 2
Table of yields at MSY: Y^*_{MSY}, Y^*_{MSY1}, ΔY^*_{MSY}, $\%\Delta Y^*_{MSY}$ with respect to the proportion of prey in patch 1, with parameter set: $K_1 = 75$, $K_2 = 5$, $D = 5$, $r_1 = 0.5$, $r_2 = 2.5$, $a = 2$, $e = 0.5$, $d = 0.5$.

u	Y^*_{MSY}	Y^*_{MSY1}	ΔY^*_{MSY}	$\%\Delta Y^*_{MSY}$
0.91	2.57	2.04	0.53	25.91%
0.92	2.65	2.04	0.61	29.64%
0.93	2.70	2.04	0.66	32.27%
0.94	2.73	2.04	0.68	33.48%
0.95	2.71	2.04	0.67	32.94%
0.96	2.66	2.04	0.62	30.38%
0.97	2.57	2.04	0.52	25.67%

exists a stable positive equilibrium, Fig. 12. Fig. 13 presents function $Y^*(E)$ with respect to E. In that case, we compare the productivity of the fishery of the system of connected sites to the productivity of isolated site 1. Our simulations have shown that for isolated patch 1, there also exists a stable equilibrium. The maximum yield (MSY) for coupled patches shows a maximum at about $Y^* = 2.71$, see Fig. 13 while the yield of isolated patch 1 at MSY is about $Y^*_1 = 2.04$, see Fig. 14. In this example, we check that the maximum yield at MSY for coupled patches is greater than the maximum yield (MSY) for isolated patch 1.

In order to have a positive yield excess, it is needed to maintain a large proportion of prey u in patch 1. Table 2 shows results for the same set of parameters : $K_1 = 75$, $K_2 = 5$, $D = 5$, $r_1 = 0.5$, $r_2 = 2.5$, $a = 2$, $e = 0.5$, $d = 0.5$ but for different values of the proportion of prey u in patch 1 ranging from 0.89 to 0.99. In that example, the yield excess in percentage is defined as $\%\Delta Y^*_{MSY} = \frac{100\Delta Y^*_{MSY}}{Y^*_{MSY1}}$. The maximum of yield excess in percentage is still obtained when $u = 0.94$. Interestingly, in this example, the proportion of prey in the two sites that maximizes the excess yield corresponds again to the IFD. Indeed, at IFD, we should have a proportion of prey on site 1 equal to $u = \frac{K_1}{K_1+K_2} = 0.9375$. As a consequence, we have shown in this case that it is useful to connect the two sites. This result is still expected insofar as the effect of a refuge for the prey is favorable to its predator.

6. Concluding remarks

In this work, we studied several fishery models at two sites connected by fast fish migrations. In the first part we considered the simplest fishing model with a single species of fish exploited on two fishing sites. We have assumed that the fish obey a logistic type growth at each fishing site. It is known that by connecting the two sites with fast constant migration rates, the total equilibrium population at the two sites can be greater than the sum of the carrying capacities of each site. However, we have shown that the optimal total catch at MSY on the two connected fishing sites is always less than or equal to the sum of the optimal catches on each of the isolated sites. This result can be seen as negative but constitutes in our eyes an interesting result.

In the next part, we considered a simple prey–predator community of fish. We considered a predator fish that feeds on another fish species. We further assumed that only predator fish are caught and not their prey. We have assumed that the prey fish obey a logistic type growth at each site. In this case, we got the opposite result as in the previous part. At MSY, the total catch may be greater than the sum of the catches at the two isolated fishing sites. This result is obtained in the case of a Lotka–Volterra (type I) or Holling (type II) functional response for the prey–predator model. In the last part, we have discussed two methods of managing a system of two fishing sites. In the first example, the manager installs artificial reefs in one of the two fishing sites. In the second example, it creates a refuge for the prey in the second patch. The first example considers a type I functional response and the second one of type II. In both cases, the total optimal catch of the connected sites can be greater than the sum of the catches on the isolated sites. To achieve this result, it is necessary to connect a fishing site with a large

carrying capacity and a low prey growth rate to a site with a small carrying capacity but a higher growth rate. It is therefore necessary to connect by fast migration two heterogeneous sites for the prey.

In the future, we could generalize our work to a network of $N > 2$ fishing sites connected by fish migrations. We would also like to study the case with two different fishing efforts at each site and find the MSY. We want to mention previous works concerning multi-site fisheries connected by migrations where the number and size of fishing sites allowing to optimize the fishing yield has been researched as well as the effects of marine protected areas, (Moussaoui et al., 2014; Bensenane et al., 2013; Auger et al., 2010) and the effects of artificial reefs (Brochier et al., 2021). In the case of the Holling type II functional response, we have limited our study to the case where there exists a stable interior prey–predator equilibrium. An interesting perspective would be to generalize the method to the case of periodic solutions by using averaging methods along a stable limit cycle.

In this work, we have considered potential application examples with very simplified models compared to reality, the example of sardinella and tuna as well as the example of a fishing site and a mangrove. In perspective, we would like to develop a concrete example with marine biologists by considering a more complex and realistic mathematical model. We could also consider an application to a fish farm with different areas and basins connected to each other with the objective of increasing total productivity.

CRediT authorship contribution statement

Pierre Auger: Study conception and design, Analysis and interpretation of results, Writing – original draft. **Bob Kooi:** Study conception and design, Analysis and interpretation of results, Writing – original draft. **Ali Moussaoui:** Study conception and design, Analysis and interpretation of results, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Maximum sustainable yield

A.1. Maximum sustainable yield in the case of an harvested population growing logistically

Let us recall some results about the logistic equation with harvesting, (Murray, 2002) :

$$\frac{dB}{dt} = rB(1 - \frac{B}{K}) - EB \tag{72}$$

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

$$Y^*(E) = EB^* = KE(1 - \frac{E}{r}) \tag{73}$$

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 "Maximum Sustainable Yield" (MSY). The corresponding value of the stable non-trivial positive equilibrium reads as follows:

$$B_{MSY}^* = K(1 - \frac{E_{MSY}^*}{r}) = \frac{K}{2} \tag{74}$$

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

$$Y_{MSY}^* = E_{MSY}^* B_{MSY}^* = \frac{rK}{4} \tag{75}$$

This yield value is the maximum sustainable yield (MSY) according to the chosen set of parameters and is achieved when the fishing effort E is chosen to be equal to half of the growth rate r of the harvested population.

A.2. Maximum sustainable yield for an harvested predator feeding from a prey

We consider the next prey–predator model with constant harvesting :

$$\frac{dB}{dt} = rB(1 - \frac{B}{K}) - aBP \tag{76}$$

$$\frac{dP}{dt} = eaBP - dP - EP \tag{77}$$

where $B(t)$ is the prey (resource) biomass and $P(t)$ the predator biomass at time t. The MSY study was done in Legovic et al. (2011). In this model, the resource grows logistically with growth rate r and carrying capacity K. The predator feeds from the resource and is harvested at a constant rate (fishing effort) E. Parameter a is the predation parameter and e the conversion efficiency of the prey biomass into predator biomass. Parameter d is the natural death rate of the predator. This model is a classical Lotka–Volterra model with type I functional response, called the Lotka–Volterra–Verhulst model with predator harvesting. It has three equilibria $(0,0)$, $(K,0)$ and (B^*, P^*) such as:

$$B^* = \frac{(d+E)}{ea} \tag{78}$$

$$P^* = \frac{r}{a}(1 - \frac{(d+E)}{eaK}) \tag{79}$$

The trivial equilibrium $(0,0)$ is always unstable. Assuming that $eaK > d$ and $E < eaK - d$, the coexisting equilibrium (B^*, P^*) belongs to the positive quadrant in the phase plane and is globally asymptotically stable for any positive initial condition. The total harvesting yield reads:

$$Y^*(E) = EP^* = \frac{rE}{a}(1 - \frac{(d+E)}{eaK}) \tag{80}$$

Now we look for the fishing effort that leads to the maximum yield. The yield has a maximum when $\frac{dY^*(E)}{dE} = 0$ i.e. for $E_{MSY}^* = \frac{(eaK-d)}{2}$. Choosing this particular fishing effort, we maximize the catch corresponding to the Maximum Sustainable Yield (MSY). The corresponding stable equilibrium is (B_{MSY}^*, P_{MSY}^*) such as:

$$B_{MSY}^* = \frac{(d+E_{MSY}^*)}{ea} = \frac{d+eaK}{2ea} \tag{81}$$

$$P_{MSY}^* = \frac{r}{a}(1 - \frac{(d+E_{MSY}^*)}{eaK}) = \frac{r}{2a}(1 - \frac{d}{eaK}) \tag{82}$$

A simple calculation leads to the maximum sustainable yield:

$$Y_{MSY}^* = E_{MSY}^* P_{MSY}^* = \frac{r}{4ea^2K}(eaK - d)^2 \tag{83}$$

Appendix B. Condition of positivity of the excess yield

Let us remember that the maximum yield Y_{MSY}^* for the system of the two connected patches by fast migrations is given by the next expression:

$$Y_{MSY}^* = \frac{r}{4ea^2K}(eaK - d)^2 \tag{84}$$

and it must be compared to the maximum yields at MSY for patch 1:

$$Y_{MSY1}^* = \frac{r_1}{4ea_1^2K_1}(ea_1K_1 - d)^2 \tag{85}$$

and patch 2:

$$Y_{MSY2}^* = \frac{r_2}{4ea_2^2K_2}(ea_2K_2 - d)^2 \tag{86}$$

where the global growth rate is $r = r_1u + (1-u)r_2$, the global carrying capacity $K = \frac{K_1K_2(r_1u+r_2(1-u))}{(K_2r_1u^2+r_2K_1(1-u)^2)}$ and the global predation parameter $a = a_1uv + (1-u)(1-v)a_2$.

The condition to have a positive excess yield ΔY_{MSY}^* is :

$$Y_{MSY}^* > Y_{MSY1}^* + Y_{MSY2}^* \tag{87}$$

Consider a heterogeneous case:

$$K_2 = \alpha K_1 \tag{88}$$

$$r_2 = \beta r_1 \tag{89}$$

$$a_2 = \gamma a_1 \tag{90}$$

where α, β and γ are positive parameters. Heterogeneity means that α is small (respectively large) i.e. the carrying capacity of patch 2 is small (respectively large) compared to that of patch 1 and similarly β and γ with respect to growth rates and predator efficiency.

After substitution, parameters of the aggregated model become:

$$r = r_1(u + \beta(1-u)) \tag{91}$$

$$K = \frac{\alpha K_1(u + \beta(1-u))}{(\alpha u^2 + \beta(1-u)^2)} \tag{92}$$

$$a = a_1(uv + \gamma(1-u)(1-v)) \tag{93}$$

By replacing in the expressions of the yields, it comes:

$$Y_{MSY}^* = \frac{r_1}{4ea_1^2\alpha K_1}\frac{(\alpha u^2 + \beta(1-u)^2)}{(uv + \gamma(1-u)(1-v))}$$
$$\times (ea_1\alpha K_1\frac{(u+\beta(1-u))(uv+\gamma(1-u)(1-v))}{(\alpha u^2 + \beta(1-u)^2)} - d)^2 \tag{94}$$

$$Y_{MSY1}^* = \frac{r_1}{4ea_1^2K_1}(ea_1K_1 - d)^2 \tag{95}$$

$$Y_{MSY2}^* = \frac{\beta r_1}{4e\gamma^2a_1^2\alpha K_1}(e\gamma a_1\alpha K_1 - d)^2 \tag{96}$$

After simplification, we obtain the following general condition to have a positive excess yield ΔY_{MSY}^* :

$$\frac{(\alpha u^2 + \beta(1-u)^2)}{\alpha(uv + \gamma(1-u)(1-v))}(ea_1\alpha K_1\frac{(u+\beta(1-u))(uv+\gamma(1-u)(1-v))}{(\alpha u^2 + \beta(1-u)^2)} - d)^2 \tag{97}$$

greater than:

$$(ea_1K_1 - d)^2 + \frac{\beta}{\gamma^2\alpha}(e\gamma a_1\alpha K_1 - d)^2 \tag{98}$$

Our numerical simulations showed that the excess yield increases when the prey and the predator are similarly distributed on the two sites, i.e. $u = v$, which leads to the following inequality:

$$\frac{(\alpha u^2 + \beta(1-u)^2)}{\alpha(u^2 + \gamma(1-u)^2)}(ea_1\alpha K_1\frac{(u+\beta(1-u))(u^2+\gamma(1-u)^2)}{(\alpha u^2 + \beta(1-u)^2)} - d)^2$$

$$> (ea_1 K_1 - d)^2 + \frac{\beta}{\gamma^2 \alpha}(e\gamma a_1 \alpha K_1 - d)^2 \qquad (99)$$

Our numerical simulations also showed that to obtain a positive excess yield, it is useful to consider an asymmetric distribution of prey and predator. Consequently, let us consider the case where u is small, for instance $u = 0.1$. We will now make some approximations neglecting terms u^2 and approximating terms $(1 - u)^2$ by $(1 - 2u)$ leading to:

$$\frac{\beta}{\alpha\gamma}(ea_1 \alpha\gamma K_1 \frac{(u + \beta(1 - u))}{\beta} - d)^2 > (ea_1 K_1 - d)^2 + \frac{\beta}{\gamma^2 \alpha}(e\gamma a_1 \alpha K_1 - d)^2 \quad (100)$$

Furthermore, let us choose $\beta = \gamma \gg 1$ and $\alpha = \frac{1}{\gamma}$. These conditions mean that the two sites are very different. Prey growth rate and predator efficiency are large in patch 2 compared to patch 1, while prey carrying capacity is small in site 2 compared to patch 1. Thereby, the inequality simplifies:

$$\beta(ea_1 K_1 \frac{(u + \beta(1 - u))}{\beta} - d)^2 > (ea_1 K_1 - d)^2 + \frac{\beta}{\gamma}(ea_1 K_1 - d)^2 \qquad (101)$$

or else:

$$(ea_1 K_1 \frac{(u + \beta(1 - u))}{\beta} - d)^2 > (\frac{1}{\beta} + \frac{1}{\gamma})(ea_1 K_1 - d)^2 \qquad (102)$$

As a numerical example, let us choose a very heterogeneous case $\beta = \alpha = 100$, then $\alpha = 0.01$. Under these conditions, the right hand side is small of the order of $0.02(ea_1 K_1 - d)^2$ while the left hand side is a bit less but of the order of $(ea_1 K_1 - d)^2$. Consequently, under these conditions of strong heterogeneity with an asymmetrical distribution, the inequality is checked. The previous condition remains fairly general and valid for all values of the other parameters. However, in order to ensure the coexistence of the prey and the predator on isolated patch 1, we must choose parameters verifying that the equilibrium predator population is positive:

$$ea_1 K_1 > d \qquad (103)$$

The condition being the same on patch 2:

$$ea_2 K_2 > d \qquad (104)$$

as $ea_2 K_2 = e\alpha\gamma a_1 K_1$ and $\alpha\gamma = 1$. In practice, if the local parameters on patch 1 are known, it would be possible to find the conditions on parameters α, β and γ for which the excess yield can be optimum.

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