



**HAL**  
open science

# The Effect of Connecting Sites in the Environment of a Harvested Population

Rafael Bravo de la Parra, Jean-Christophe Poggiale, Pierre Auger

► **To cite this version:**

Rafael Bravo de la Parra, Jean-Christophe Poggiale, Pierre Auger. The Effect of Connecting Sites in the Environment of a Harvested Population. *Mathematical Modelling of Natural Phenomena*, 2023, 18, pp.4. 10.1051/mmnp/2023004 . hal-04015209

**HAL Id: hal-04015209**

**<https://amu.hal.science/hal-04015209>**

Submitted on 5 Mar 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Copyright

# The effect of connecting sites in the environment of a harvested population

Rafael Bravo de la Parra<sup>a,\*</sup>, Jean-Christophe Poggiale<sup>b</sup>, Pierre Auger<sup>c</sup>

<sup>a</sup>*U.D. Matemáticas, Universidad de Alcalá, Edificio de Ciencias, 28871, Alcalá de Henares, Spain*

<sup>b</sup>*CNRS/INSU, Université de Toulon, IRD, Mediterranean Institute of Oceanography (MIO) UM 110, Aix Marseille Université, Campus de Luminy, 13288, Marseille, France*

<sup>c</sup>*UMMISCO, Sorbonne Université, Institut de Recherche pour le Développement, IRD, F-93143, Bondy, France*

---

## 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.

*Keywords:* multisite fishery, Gordon-Schaefer model, time scales, maximum sustainable yield

---

\*Corresponding author

*Email addresses:* [rafael.bravo@uah.es](mailto:rafael.bravo@uah.es) (Rafael Bravo de la Parra), [jean-christophe.poggiale@univ-amu.fr](mailto:jean-christophe.poggiale@univ-amu.fr) (Jean-Christophe Poggiale), [pierre.auger@ird.fr](mailto:pierre.auger@ird.fr) (Pierre Auger)

## 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), (Hilborn et al. , 2006), 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, (Fonteneau et al. , 2000) and (Dagorn et al. , 2007). 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 (Polovina and Sakai , 1989) and attract fish (Bortone , 1998). 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 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), (Bernstein et al. , 1999) and (Fretwell and Lucas , 1970).

In the case of a single fishing site, without adding economic assumptions, it is usual to consider the Schaefer model, (Schaefer , 1957; Clark , 1990):

$$N' = rN\left(1 - \frac{N}{K}\right) - qEN \quad (1)$$

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

28 stock level, with  $E$  denoting the constant fishing effort and constant  $q$  being the catchability  
 29 coefficient. If  $r - qE > 0$ , for any positive initial condition,  $N(t)$  tends to an equilibrium  
 30  $N^* = K(1 - qE/r)$ . It is also well known (Clark , 1990) that the yield at equilibrium  
 31  $Y(E) = qK(1 - qE/r)E$ , as function of  $E$ , attains its maximum for  $E_{MSY} = r/(2q)$ . The  
 32 corresponding yield, called maximum sustainable yield (MSY), is  $Y_{MSY} = rK/4$ , and the  
 33 equilibrium stock biomass is  $N_{MSY} = K/2$ .

34 In (Auger et al. , 2022) a simple spatialized version of Schaefer's model is studied.  
 35 Only two sites are considered and the local dynamics is of the form (1). Furthermore, the  
 36 fish stock move between the two sites on a faster time scale than that associated with local  
 37 dynamics:

$$\begin{aligned} \frac{dN_1}{d\tau} &= m_2N_2 - m_1N_1 + \varepsilon\left(r_1N_1\left(1 - \frac{N_1}{K_1}\right) - qE_1N_1\right) \\ \frac{dN_2}{d\tau} &= m_1N_1 - m_2N_2 + \varepsilon\left(r_2N_2\left(1 - \frac{N_2}{K_2}\right) - qE_2N_2\right) \end{aligned} \quad (2)$$

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

43 As a consequence of the existence of two time scales, the two-dimensional model (2)  
 44 can be analyzed through a one-dimensional Schaefer-type model. The MSY of (2) is easily  
 45 approximated with the help of this one-dimensional model. From it, it is straightforward to  
 46 compare the MSY for connected and isolated sites. In this latter case the MSY is calculated  
 47 just by adding the two local MSY. An important result obtained in (Auger et al. , 2022)  
 48 is that the MSY for a system of two connected fishing sites is always less than or equal  
 49 to the MSY of the system with isolated sites. Thus, there is no interest in facilitating the  
 50 connection between the sites because this would not increase the MSY of the system. This  
 51 is the conclusion when we have not yet brought economic issues into the model.

52 Fishing boats also travel between the various fishing areas. The fishing boats are evenly  
 53 distributed among the various fishing areas, avoiding having to meet all at the same time

54 on the same site. The distribution of the boats in the fishing fleet on the different sites  
55 has an effect on the overall catch made on the multisite fishery. In a global way, the  
56 combined distribution of fish stock and fishing vessels among the various fishing areas has  
57 a significant effect on the overall catch of the multisite fishery, (Brochier et al. , 2021).

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

68 To deal with this question it is necessary to introduce the economy in Schaefer's model.  
69 A widespread way of doing this is to consider fishing effort as a system variable whose rate  
70 of change is proportional to the benefit, i.e., the difference between revenue and cost. We  
71 use Gordon's model of an open access fishery together with Schaefer's model to approach  
72 the analysis that we propose in this work. We want to study the conditions for a network  
73 of discrete fishing sites, connected to each other by fast displacements, to obtain a higher  
74 or lower fishing yield than if the sites were isolated.

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

81 We assume that the fishing sites are relatively close to each other allowing fast move-  
82 ments of the stock and the fishing fleet between these various fishing areas. When the sites

83 are close enough, it makes sense to consider that the operating costs are the same in all  
84 fishing areas, same wages, taxes, fuel and maintenance costs as well as minimum profit  
85 required. The government or the national fisheries management institution has no reason  
86 to impose different taxes on fishing sites close to each other.

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

## 96 **2. A single-site harvested population model**

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

$$\begin{aligned} \frac{dN}{dt} &= rN\left(1 - \frac{N}{K}\right) - qEN \\ \frac{dE}{dt} &= pqEN - cE \end{aligned} \tag{3}$$

106 We refer to (3) as the basic Gordon-Schaefer model. It has the same form as the Lotka-  
107 Volterra predator-prey model with prey logistic growth (Iannelli and Pugliese , 2014). The

108 asymptotic behaviour of its solutions is simply expressed. If  $c < pqK$ , i.e., the benefit is  
 109 positive when the stock is at the carrying capacity, then all positive solutions of the system  
 110 tend to the so-called bionomic equilibrium:

$$N^* = \frac{c}{pq}, \quad E^* = \frac{r}{q} \left( 1 - \frac{c}{pqK} \right), \quad (4)$$

111 with an associated yield

$$Y^* = \frac{rc}{pq} \left( 1 - \frac{c}{pqK} \right). \quad (5)$$

112 In the open-access fishery, Gordon-Schaefer model, the fishery effort and the stock tend to  
 113 reach an equilibrium at the level at which the benefit vanishes (Clark , 1990), as the  $E$   
 114 equation imposes.

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

119 In model (3), the value of  $c$  that maximizes the equilibrium yield (5) is

$$c_{opt} = \frac{1}{2}pqK, \quad (6)$$

120 obtaining

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

121 So, we recuperate the situation of MSY (1) of the constant effort case.

122 Notice that  $c_{opt}$  is one half of the maximum cost yielding positive benefit. It leads the  
 123 stock  $N_{opt}$  to one half of the environment carrying capacity  $K$ , that is the population size  
 124 with the largest growth rate. Both, the optimal cost  $c_{opt}$  and the stock  $N_{opt}$ , as well as  
 125 the optimal yield  $Y_{opt}$  are proportional to  $K$ . Nevertheless, the corresponding effort  $E_{opt}$   
 126 depends on the ratio intrinsic growth rate to catchability and it is independent of  $K$ . A  
 127 consequence of this can be considered through the following example. A zone with carrying  
 128 capacity  $K$  is managed in two different forms, as a whole and divided into two equal and

129 independent zones with carrying capacities  $K/2$ . In both cases the management follows  
 130 the dynamics of open-access fishery with chosen optimal cost. The global result is that at  
 131 equilibrium the yield and the stock are equal in the two strategies, whereas the optimal  
 132 cost is double in the first one and the effort is double in the second one.

### 133 3. A two-site harvested population model

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

137 We begin by limiting the multisite environment to two sites. We will extend this for an  
 138 arbitrary number of sites later on. In each site, the stock-effort dynamics is ruled by a local  
 139 basic Gordon-Schaefer model (3). The movements between sites are described by constant  
 140 rates and in a first approach, are considered fast in comparison to the local dynamics.

141 Thus, let us consider the following model:

$$\begin{aligned}
 \frac{dN_1}{d\tau} &= m_2 N_2 - m_1 N_1 + \varepsilon \left( r_1 N_1 \left( 1 - \frac{N_1}{K_1} \right) - q E_1 N_1 \right) \\
 \frac{dN_2}{d\tau} &= m_1 N_1 - m_2 N_2 + \varepsilon \left( r_2 N_2 \left( 1 - \frac{N_2}{K_2} \right) - q E_2 N_2 \right) \\
 \frac{dE_1}{d\tau} &= \mu_2 E_2 - \mu_1 E_1 + \varepsilon (pq E_1 N_1 - c E_1) \\
 \frac{dE_2}{d\tau} &= \mu_1 E_1 - \mu_2 E_2 + \varepsilon (pq E_2 N_2 - c E_2)
 \end{aligned} \tag{7}$$

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

149 We proceed now to compare the maximum sustainable yield in two different cases. In  
 150 the first one, that we call *connected sites* case, stock and effort movements are allowed



151 so that the dynamics is defined through system (7). In the second one, *unconnected sites*  
 152 case, there is no stock and effort movements and, therefore, the dynamics is represented  
 153 by the following independent systems, both with the form of (3), for  $i = 1, 2$ :

$$\begin{aligned}\frac{dN_i}{dt} &= r_i N_i \left(1 - \frac{N_i}{K_i}\right) - q E_i N_i \\ \frac{dE_i}{dt} &= p q E_i N_i - c E_i\end{aligned}\tag{8}$$

154 System (7) is not of the form of system (3) but it can be reduced to one of this form.  
 155 The fact that it includes two time scales allows us to apply the reduction method developed  
 156 in (Auger et al. , 2008a,b). It consists in a sort of decoupling the fast and the slow parts of  
 157 the system. The fast part of the system corresponds to the movements dynamics and let  
 158 invariant the total stock  $N = N_1 + N_2$  and the total fishing effort  $E = E_1 + E_2$ . Moreover,  
 159 it makes the proportions of stock and effort in each site rapidly tend to an equilibrium.  
 160 The equilibrium proportions for the stock are

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

161 and for the effort

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

162 Assuming that movements have attained their equilibrium proportions, we can write a  
 163 reduced system for the total stock and effort in terms of the slow time variable  $t = \varepsilon \tau$ . We  
 164 add the two stock equations and the two effort equations, and substitute each of the state  
 165 variables by the corresponding total variable times the associated site proportion, i.e., for  
 166  $i = 1, 2$ ,  $N_i = N u_i$  and  $E_i = E v_i$ . The result is the following basic Gordon-Schaefer model:

$$\begin{aligned}\frac{dN}{dt} &= \bar{r} N \left(1 - \frac{N}{\bar{K}}\right) - \bar{q} E N \\ \frac{dE}{dt} &= p \bar{q} E N - c E\end{aligned}\tag{9}$$

167 whose parameters,  $\bar{r} = r_1 u_1 + r_2 u_2$ ,  $\bar{K} = \frac{(r_1 u_1 + r_2 u_2) K_1 K_2}{r_2 u_2^2 K_1 + r_1 u_1^2 K_2}$  and  $\bar{q} = q(u_1 v_1 + u_2 v_2)$ , include  
 168 the local parameters and the equilibrium stock and effort proportions on sites. The so-

169 called aggregated model (9) possesses a positive globally asymptotically stable equilibrium  
 170 provided that  $\bar{K} > \frac{c}{p\bar{q}}$ . It is given by

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

171 The yield at equilibrium is thus

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

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

175 To compare the maximum sustainable yield in the connected and unconnected sites  
 176 cases, we now consider the yield at equilibrium maximized as a function of a single cost.  
 177 In the first case using system (9) and in the second case with the help of systems (8).

### 178 3.1. Connected sites

179 The maximum sustainable yield as a function of the cost, in the case with fast move-  
 180 ments of the stock and the efforts can be obtained by using (6) in system (9). For the  
 181 cost

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

182 the maximum yield is

$$Y_{opt} = \frac{1}{4} \bar{r}\bar{K} = \frac{1}{4} \frac{(r_1u_1 + r_2u_2)^2 K_1K_2}{r_2u_2^2K_1 + r_1u_1^2K_2}. \quad (10)$$

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

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

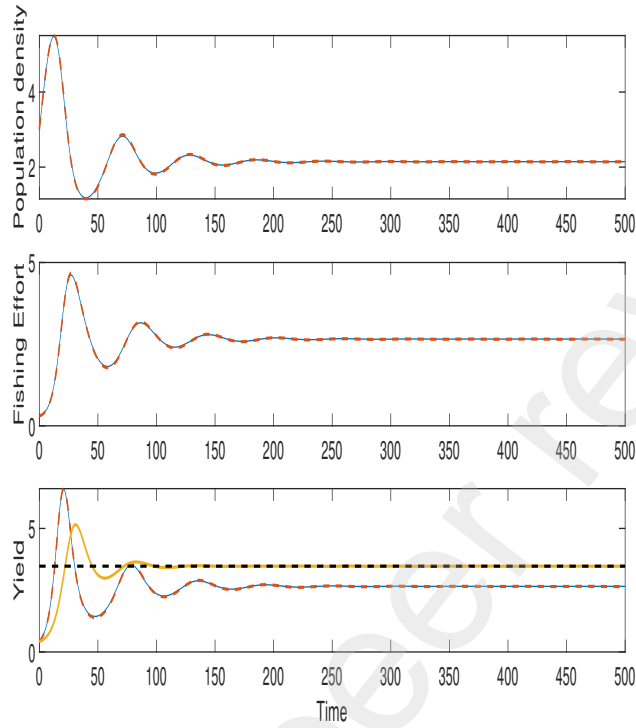


Figure 1: Comparison between the complete model (7) and the aggregated model (9) for the following parameters values:  $m_1 = 2$ ,  $m_2 = 1$ ,  $\mu_1 = 2$ ,  $\mu_2 = 3$ ,  $r_1 = 1$ ,  $r_2 = 2$ ,  $K_1 = 5$ ,  $K_2 = 5$ ,  $q = 1$ ,  $p = 1$ , and  $c = 1$ .  $\varepsilon = 0.1$  is chosen.

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  $Y_{opt} = rK/4$ .

186 The maximum yield (10) is strongly dependent on the equilibrium distribution of the  
 187 stock to which the movements give rise. Let us show this with the help of a simple case. If  
 188 we assume two biologically identical sites,  $r_1 = r_2 = r$  and  $K_1 = K_2 = K/2$ , then we have

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

189 If the stock is homogeneously distributed,  $u_1 = 1/2 = u_2$ , then  $Y_{opt} = rK/4$ , that corre-

190 sponds to the MSY considering a single stock with biological parameters  $r$  and  $K$ . Nev-  
 191 ertheless, if  $u_1$  approaches 1 and, thus,  $u_2$  approaches 0 (or vice versa), i.e., the stock is  
 192 mainly established in the first site (or the second one), then  $Y_{opt}$  tends to  $rK/8$ . Uneven  
 193 stock distribution could almost halve the maximum yield.

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

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

196 Its derivative can be expressed as

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

197 and, therefore, its sign just depends on expression  $K_1 - (K_1 + K_2) u_1$ . The maximum is  
 198 attained for  $u_1 = \frac{K_1}{K_1 + K_2}$ , that implies  $u_2 = \frac{K_2}{K_1 + K_2}$ . This stock distribution, propor-  
 199 tional to the sites carrying capacities, is known in ecological literature as the Ideal Free  
 200 Distribution (IFD) Fretwell and Lucas (1970). The corresponding yield is

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

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

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

202 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  
 203 its maximum, at the IFD, and then decreases to  $\frac{1}{4} r_1 K_1$ , for  $u_1 = 1$  (the whole stock living  
 204 in site 1).

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

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

208 *3.2. Unconnected sites*

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

212 In this case, the yield of the system is the sum of the yields on each separate site. Using  
 213 expression (5) in both systems (8), one gets:

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

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

$$Y_{S,opt} = \frac{(r_1 + r_2)^2 K_1 K_2}{4(r_1 K_2 + r_2 K_1)}. \quad (11)$$

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

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

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

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

218 In the previous case of connected sites we showed that the MSY (10) is strongly depen-  
 219 dent on equilibrium stock distribution. We found that to maximize MSY this distribution  
 220 must be the IFD. In this case of unconnected sites the equilibrium stock distribution does  
 221 not apply because they are independent. Nevertheless, we are showing that how the total  
 222 carrying capacity of the system,  $K = K_1 + K_2$ , is distributed between the sites does play  
 223 a relevant role.

224 We start approaching the question in a simple case. Let us assume  $r_1 = r_2 = r$ , and  
 225 represent the total carrying capacity distribution by means of the fraction  $\alpha \in (0, 1)$  of  $K$

226 in the first site, i.e.,  $K_1 = \alpha K$  and  $K_2 = (1 - \alpha)K$ . Substituting these values in (11) we  
 227 get

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

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

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

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

232 This function also tends to zero when  $\alpha$  tends to zero or one. Its maximum is attained for

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

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

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

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

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

### 238 3.3. Comparison of the MSY for connected and unconnected sites

239 To compare the MSY obtained in the two cases, connected and unconnected sites, we  
 240 define the ratio  $\rho_Y$  of  $Y_{opt}$  (10) to  $Y_{S,opt}$  (11),

$$\rho_Y = \frac{Y_{opt}}{Y_{S,opt}} = \frac{(r_1 K_2 + r_2 K_1)(r_1 u_1 + r_2 u_2)^2}{(r_1 + r_2)^2 (r_2 u_2^2 K_1 + r_1 u_1^2 K_2)}. \quad (12)$$

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

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

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

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

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

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

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

$$\frac{1}{2} \text{ and } \bar{u}_1 := \frac{(r_1 + 2r_2)K_1 - r_2K_2}{2(r_2K_1 + r_1K_2)}.$$

257 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  
 258 we have then

259  $\rho_Y > 1$  if and only if one of the next two conditions is met

$$K_1 > K_2 \text{ and } u_1 \in \left( \frac{1}{2}, \min\{\bar{u}_1, 1\} \right) \quad (13)$$

$$K_1 < K_2 \text{ and } u_1 \in \left( \max\{\bar{u}_1, 0\}, \frac{1}{2} \right) \quad (14)$$

260 We illustrate the results obtained with Figure 2.

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

$$\rho_Y = \left( \frac{\rho_r u_1 + u_2}{\rho_r + 1} \right)^2 \frac{\rho_r + \rho_K}{\rho_r u_1^2 + \rho_K u_2^2}. \quad (15)$$

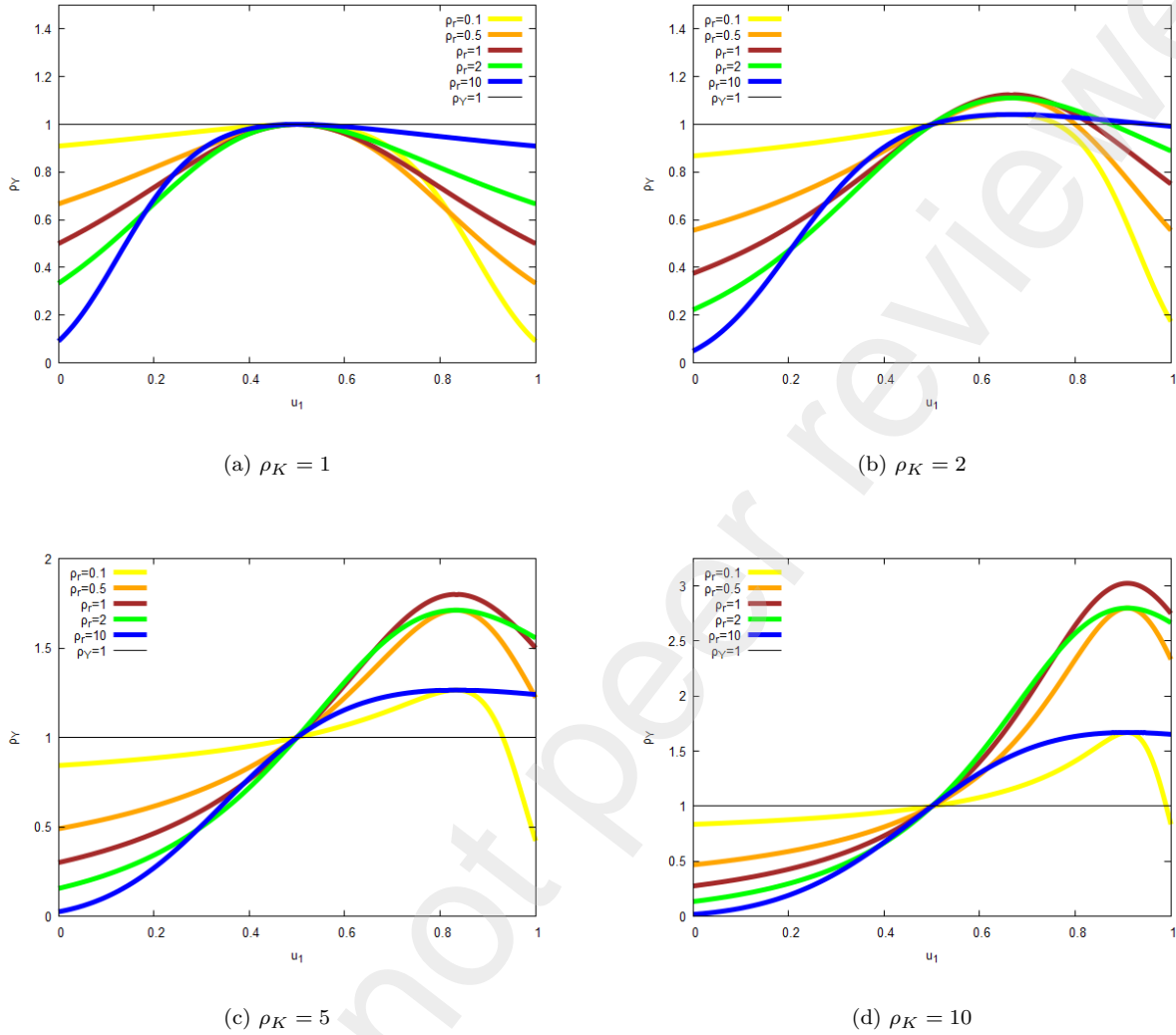


Figure 2: Graphs of  $\rho_Y$  as a function of  $u_1$  for different values of  $\rho_K$ : 1, 2, 5, and 10; and different values of  $\rho_r$ : 0.1, 0.5, 1, 2, and 10.

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

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

264 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  
 265 the value of  $\rho_Y$  as a function of  $u_1$  ( $u_2 = 1 - u_1$ ) for  $\rho_K = 1$  and different values of  $\rho_r$ .

266 The rest of the figures in Figure 2 make this same representation for three increasing  
 267 values of  $\rho_K$ . In them you can clearly see the range of values of  $u_1$  (13), the fraction of



268 the stock that stabilizes in site 1, for which  $\rho_Y > 1$ , i.e., for which the optimal yield is  
 269 higher if the sites are connected. It can be seen that in all cases the maximum of  $\rho_Y$  is  
 270 approximately reached when  $u_1$  represents the IFD, that is, for  $u_1 = \rho_K/(1 + \rho_K)$ . We  
 271 note that to obtain  $\rho_Y > 1$  it is necessary for the equilibrium stock distribution to have  
 272 more weight in the site with the highest carrying capacity. In Figure 2 we see that for any  
 273  $u_1 < 1/2$  the site connection does not improve the maximum yield, i.e.,  $\rho_Y < 1$ . Concerning  
 274 the role of the intrinsic growth ratio,  $\rho_r$ , we observe that the maximum value of  $\rho_Y$ , for  
 275 fixed  $\rho_K$ , is obtained for  $\rho_r = 1$ , that is, when  $r_1 = r_2$ .

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

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

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

282 In each site, the stock-effort dynamics is ruled by a local basic Gordon-Schaefer model  
 283 (3).

284 In the case of connected sites, we assume that movements between sites are fast com-  
 285 pared to local dynamics. They are described by constant rates. Let us denote  $m_{ij}$  and  $\mu_{ij}$ ,  
 286  $i \neq j$  and  $i, j \in \{1, \dots, L\}$ , the transition rates from site  $j$  to site  $i$ , for stock and effort  
 287 respectively. To lighten the model writing, let us define, for  $i \in \{1, \dots, L\}$ ,

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

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

289 The extension of model (7) to an L-site environment reads as follows:

$$\begin{aligned}
 \frac{dN_i}{d\tau} &= \sum_{j=1}^L m_{ij} N_j + \varepsilon \left( r_i N_i \left( 1 - \frac{N_i}{K_i} \right) - q E_i N_i \right), \\
 \frac{dE_i}{d\tau} &= \sum_{j=1}^L \mu_{ij} E_j + \varepsilon (pq E_i N_i - c E_i) \quad , \quad i = 1, \dots, L.
 \end{aligned}
 \tag{16}$$

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

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

$$\begin{aligned}
 \frac{dN_i}{dt} &= r_i N_i \left( 1 - \frac{N_i}{K_i} \right) - q E_i N_i \\
 \frac{dE_i}{dt} &= pq E_i N_i - c E_i
 \end{aligned}
 \tag{17}$$

297 Assuming that matrices  $M_1 = (m_{ij})$  and  $M_2 = (\mu_{ij})$  are irreducible, the same method  
 298 we used to reduce system (7), (Auger et al. , 2008a,b), apply to system (16). The inter-  
 299 pretation of the irreducibility of a matrix in this context is that the connections between  
 300 sites allow to establish a path joining any site to any other. The movements dynamics let  
 301 invariant the total stock  $N = N_1 + \dots + N_L$  and the total fishing effort  $E = E_1 + \dots + E_L$ .  
 302 Moreover, it makes the proportions of stock and effort in each site rapidly tend to an equi-  
 303 librium. Let  $\bar{u} = (u_1, \dots, u_L)$  and  $\bar{v} = (v_1, \dots, v_L)$  be these equilibrium proportions for  
 304 stock and effort respectively. Vectors  $\bar{u}$  and  $\bar{v}$  are the right eigenvectors of matrices  $M_1$  and  
 305  $M_2$  associated to eigenvalue 0 and whose entries sum up to 1, see Section A.5. in Smith  
 306 and Thieme (2011) for details on this kind of matrices called quasipositive irreducible.

307 The associated reduced system for the total stock and effort in terms of the slow time

308 variable  $t = \varepsilon\tau$  is the following basic Gordon-Schaefer model:

$$\begin{aligned} \frac{dN}{dt} &= \sum_{i=1}^L \left( r_i u_i N \left( 1 - \frac{u_i N}{K_i} \right) - q v_i E u_i N \right) = \bar{r} N \left( 1 - \frac{N}{\bar{K}} \right) - \bar{q} E N \\ \frac{dE}{dt} &= \sum_{i=1}^L \left( p q v_i E u_i N - c v_i E_i \right) = p \bar{q} E N - c E \end{aligned} \quad (18)$$

309 where

$$\bar{r} = \sum_{i=1}^L u_i r_i \quad , \quad \bar{K} = \frac{\bar{r}}{\sum_{i=1}^L (u_i^2 \frac{r_i}{K_i})} \quad , \quad \bar{q} = \left( \sum_{i=1}^L (u_i v_i) \right) q. \quad (19)$$

310 To compare the maximum sustainable yield in the cases of connected and unconnected  
311 sites, we now consider the yield at equilibrium maximized as a function of a single cost. In  
312 the first case using system (18) and in the second case with the help of systems (17).

#### 313 4.1. Connected sites

314 In the case of connected sites, we apply (6), the value of the cost that maximizes the  
315 equilibrium yield in the basic Gordon-Schaefer model, to system (18), obtaining

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

316 and the maximum equilibrium yield

$$Y_{opt} = \frac{1}{4} \bar{r} \bar{K} = \frac{1}{4} \frac{\left( \sum_{i=1}^L u_i r_i \right)^2}{\sum_{i=1}^L (u_i^2 r_i / K_i)}. \quad (20)$$

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

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

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

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

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

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

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

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

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

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

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

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

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

335 4.2. Unconnected sites

336 When the sites are not connected we must consider them independently. Thus, the  
 337 yield of the system is just the sum of the yields on each separate site. Using expression (5)  
 338 in all the  $L$  systems (17), one gets:

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

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

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

341 and the maximum yield is equal to

$$Y_{S,opt} = \left( \sum_{i=1}^L r_i \right)^2 / \left( 4 \sum_{i=1}^L \frac{r_i}{K_i} \right). \quad (21)$$

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

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

343 but this need not be the case concerning the effort equilibria

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

344 In the previous case of connected sites we showed that the MSY (20) is strongly de-  
 345 pendent on equilibrium stock distribution associated to stock fast movements. When this  
 346 distribution is the IFD the maximum equilibrium yield attains its maximum. In the case of  
 347 unconnected sites movements are not considered and, therefore, it does not make sense to  
 348 speak about the equilibrium stock distribution they lead to. Nevertheless, we can consider  
 349 the distribution among sites of the total carrying capacity of the system,  $K = \sum_{i=1}^L K_i$ ,  
 350 and show that it does play a relevant role by treating a simple case.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

### 370 4.3. Comparison of $Y_{opt}$ and $Y_{S,opt}$

371 To compare the maximum yield as obtained in the two studied cases, connected and  
 372 unconnected sites, we define the ratio  $\rho_Y$  of  $Y_{opt}$  (20) to  $Y_{S,opt}$  (21),

$$\rho_Y = \frac{Y_{opt}}{Y_{S,opt}} = \frac{\left( \sum_{i=1}^L u_i r_i \right)^2 \sum_{i=1}^L (r_i / K_i)}{\left( \sum_{i=1}^L r_i \right)^2 \sum_{i=1}^L (u_i^2 r_i / K_i)}. \quad (22)$$

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

375 As it was remarked in the model with two sites,  $\rho_Y$  depends only on the biological  
 376 parameters,  $r_i$  and  $K_i$ , and on the stock movements through the equilibrium stock dis-  
 377 tribution  $u_i$ , but it does not depend on the efforts frequencies  $v_i$ . Changing the efforts  
 378 movements rates will not change the value of  $\rho_Y$ .

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

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

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

$$\frac{K_i}{K_j} r_i r_j + \frac{K_j}{K_i} r_j r_i > r_i r_j + r_j r_i \text{ if } K_i \neq K_j, \quad (23)$$

384 and the equality of both expressions holds if  $K_i = K_j$ . Now, as we can write  $\rho_Y^{IFD}$  in the  
 385 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  $i, j \in \{1, \dots, L\}$ , 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  $\rho_Y$  being bigger or less than 1. To show that unconnected sites can also lead to a larger maximum yield, let us calculate  $\rho_Y$  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  $i = 1, \dots, L$ , where  $K$  represents the total carrying capacity. The  $\rho_Y$ , 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  $\rho_Y$  approaches 1, but it can be much less than 1 if stock movements equilibrium distribution gets away from IFD.

## 5. Conclusion

In the early contribution (Freedman and Waltman, 1977), it was shown 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



406 in several other articles, (Holt , 1985; Poggiale et al. , 2005; DeAngelis and Zhang , 2014;  
407 DeAngelis et al , 2016; Arditi et al. , 2015, 2018; Zhang et al. , 2021). A condition for  
408 obtaining higher productivity from the system of two connected sites compared to the  
409 system of two isolated sites is to consider a heterogeneous environment, that is to say with  
410 two sites having different environmental properties, in particular having different growth  
411 rates and carrying capacities, (Poggiale et al. , 2005).

412

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

420

421 This problem, as we mentioned in the introduction, has already been dealt with in  
422 (Auger et al. , 2022). As can be seen in system (2), the population is harvested at a  
423 rate proportional to its size following the classical Schaefer's model. Yield optimization is  
424 performed with respect to the fishing effort parameter  $E$ . The analysis of the model offers  
425 a result that we could describe as negative. Regardless of the movement rates chosen and  
426 whether or not the sites are environmentally homogeneous, connecting the sites does not  
427 allow increasing the sum of the MSY of the unconnected sites. Equality occurs when the  
428 exploited species is distributed over the two sites according to the ideal free distribution.  
429 This result is quite general as soon as the harvested population equation includes a logistic  
430 growth term from which the catch is subtracted. Indeed, at equilibrium, the capture is  
431 equal to a logistic growth term which is always maximum when the population is at half  
432 the carrying capacity. This always leads to the same value of the catch at MSY and,  
433 therefore, to the inability to increase optimal yield by connecting sites. A positive answer  
434 is obtained in the same work (Auger et al. , 2022) considering a prey-predator community

435 of fish in the same environment, where only the predators are harvested. It is shown that  
436 the total MSY of the system can be greater with connected sites. The condition leading  
437 to this result consist in connecting a fishing site with a large prey carrying capacity and  
438 an average growth rate to a site with a small prey carrying capacity but a large growth rate.

439

440 The models analyzed in this paper includes economic factors, which were not consid-  
441 ered in (Auger et al. , 2022). The fishing effort  $E$  becomes a variable whose dynamics  
442 follow the hypothesis of the open access fishery. The non-spatialized model, (3), leads,  
443 under a certain condition, to an equilibrium of both the stock and the effort, and therefore  
444 also the yield. From this, we have chosen the cost  $c$  as a parameter with respect to which  
445 to optimize the yield. We have preferred  $c$  over other possible choices because it includes  
446 all the costs of operating a fishery, including the profit margin that the owner considers  
447 profitable. In addition, it is an element on which management can act through taxes or  
448 subsidies.

449

450 The model (3) is used as a local model to build a multisite fishery model. The man-  
451 agement of the fishery is unique and the same cost and price are established in each of  
452 the sites. When unconnected sites are considered, the model for the fishery is made up of  
453 a collection of independent systems (3). When the sites are connected, with rapid move-  
454 ments of the stock and of the fishing effort, the model (7) is proposed for two sites and, in  
455 general, for any number  $L$  of sites, the model (16). Once the maximum sustainable yield  
456 (MSY) is obtained based on the cost  $c$ , the comparison between the fishery with connected  
457 and unconnected sites based on this criterion is developed. The ratio  $\rho_Y$  between the MSY  
458 with connected sites,  $Y_{opt}$ , and with unconnected sites,  $Y_{S,opt}$ , is used to decide whether to  
459 prefer a connected fishery, if  $\rho_Y > 1$ , or an unconnected fishery, whenever  $\rho_Y < 1$ .

460

461 In the case of two sites the ratio  $\rho_Y$  depends on two other ratios, that of the carrying  
462 capacities,  $\rho_K$ , and that of the intrinsic growth rates,  $\rho_r$ , and on the equilibrium distribu-  
463 tion of the stock reflected in  $u_1$ . The rest of the parameters do not play any role. A first

464 general conclusion is that if the carrying capacities of the two sites are equal,  $\rho_K = 1$ , then  
465 for any values of  $u_1$  and  $\rho_r$  we have that  $\rho_Y \leq 1$ , with the equality valid only if  $u_1 = 1/2$ . If  
466 the two sites have the same carrying capacities, it is better to keep the sites unconnected.  
467 Another general result but in the opposite sense follows. If the equilibrium distribution of  
468 the stock coincides with the IFD then it is better to use connected sites. Figure 2 shows  
469 that whenever the carrying capacity of site 1 is greater than that of site 2,  $\rho_K > 1$ , there  
470 is an interval of values of  $u_1$ , whose left endpoint is  $1/2$  and, on the right, can be as high  
471 as 1, such that  $\rho_Y > 1$ . If the fishery can be managed so that the equilibrium distribution  
472 of the stock is in this interval, connecting the sites will give a higher MSY. Note that the  
473 best results are obtained when the equilibrium distribution of the stock is around the IFD.  
474 The values of  $\rho_Y$  obtained grow with  $\rho_K$  and are reached for values of  $\rho_r$  close to 1, i.e.  
475 equal intrinsic growth rates. A symmetric analysis is valid if the largest carrying capacity  
476 is that of site 2. Similar general conclusions can be reached in the case of  $L$  sites.

477

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

491

492 In (Zhang et al. , 2017), the authors performed experiments with aquatic plants growing

493 logistically in containers. They simulated in real world the fast migrations by transferring  
494 plants from one container to another with a periodicity of a few days. They considered  
495 a heterogeneous environment with different growth conditions from container to container  
496 of different sizes. Under these conditions, they showed that the total productivity, in  
497 terms of carrying capacities, could be greater in heterogeneous conditions rather than in  
498 homogeneous conditions. An important perspective of this work is to consider carrying  
499 out experiments of the same type making it possible to generalize the results obtained in  
500 (Zhang et al. , 2017) to the case of exploited species, either a single commercial species as  
501 in this work with an identical operating cost in all sites or in the case of fish prey-predator  
502 systems with exploitation of the predator, (Auger et al. , 2022).

### 503 **Acknowledgements**

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

### 508 **References**

- 509 Arditi, R., Lobry, C., Sari, T., 2015. Is dispersal always beneficial to carrying capac-  
510 ity? New insights from the multi-patch logistic equation. *Theor. Pop. Biol.* 106, 45–59.  
511 <https://doi.org/10.1016/j.tpb.2015.10.001>.
- 512 Arditi, R., Lobry, C., Sari, T., 2018. Asymmetric dispersal in the multi-patch logistic  
513 equation, *Theor. Pop. Biol.* 120, 11–15. <https://doi.org/10.1016/j.tpb.2017.12.006>.
- 514 Auger, P., Bravo de la Parra, R., Poggiale, J.-C., Sánchez, E., Nguyen Huu, T., 2008.  
515 Aggregation of variables and applications to population dynamics. In: Magal, P.,  
516 Ruan, S. (Eds.), *Structured Population Models in Biology and Epidemiology. Lec-  
517 ture Notes in Mathematics*, vol. 1936, Math. Biosci. Subseries. Springer, pp. 209–263.  
518 [https://doi.org/10.1007/978-3-540-78273-5\\_5](https://doi.org/10.1007/978-3-540-78273-5_5).

- 519 Auger, P., Bravo de la Parra, R., Poggiale, J.-C., Sánchez, E., Sanz, L., 2008. Aggregation  
520 methods in dynamical systems and applications in population and community dynamics.  
521 *Phys. Life. Rev.* 5, 79–105. <https://doi.org/10.1016/j.plrev.2008.02.001>.
- 522 Auger, P., Kooi, B., Moussaoui, A., 2022. Increase of maximum sustainable  
523 yield for fishery in two patches with fast migration. *Ecol. Model.* 467, 109898.  
524 <https://doi.org/10.1016/j.ecolmodel.2022.109898>.
- 525 Bernstein, C., Auger, P., Poggiale, J.-C., 1999. Predator Migration Decisions, the  
526 Ideal Free Distribution, and Predator-Prey Dynamics. *Am. Nat.* 153, 267-281.  
527 <https://doi.org/10.1086/303170>
- 528 Bortone, S. A., 1998. Resolving the attraction-production dilemma in artificial reef  
529 research: Some Yeas and Nays. *Fisheries* 23, 6–10. [https://doi.org/10.1577/1548-  
530 8446\(1998\)023;0006:RTADIA;2.0.CO;2](https://doi.org/10.1577/1548-8446(1998)023;0006:RTADIA;2.0.CO;2).
- 531 Brochier, T., Brehmer, P., Mbaye, A., Diop, M., Watanuki, N., Terashima, H., Ka-  
532 plan, D., Auger, P., 2021. Successful artificial reefs depend on getting the con-  
533 text right due to complex socio-bio-economic interactions. *Sci. Rep.-UK* 11, 16698.  
534 <https://doi.org/10.1038/s41598-021-95454-0>.
- 535 Clark, C.W., 1990 . *Mathematical Bioeconomics. The Optimal Management of Renewable*  
536 *Resources.* John Wiley & Sons.
- 537 Dagorn, L., Holland, K.N., Itano, D.G., 2007. Behavior of yellowfin (*Thunnus albacares*)  
538 and bigeye (*T. obesus*) tuna in a network of fish aggregating devices (FADs). *Mar. Biol.*  
539 (Berl.) 151(2), 595–606. <https://doi.org/10.1007/s00227-006-0511-1>.
- 540 DeAngelis, D.L., Ni, W.-M., Zhang, B., 2016. Effects of diffusion on total biomass  
541 in heterogeneous continuous and discrete-patch systems. *Theor. Ecol.* 9, 443–453.  
542 <https://doi.org/10.1007/s12080-016-0302-3>.

- 543 DeAngelis, D.L., Zhang, B., 2014. Effects of dispersal in a non-uniform environment on  
544 population dynamics and competition: a patch model approach. *Discrete Contin. Dyn.-B*  
545 19, 3087–3104. <https://doi.org/10.3934/dcdsb.2014.19.3087>.
- 546 Fonteneau, A., Ariz, J., Gaertner, D., Nordstrom, T., Pallares, P., 2000. Observed changes  
547 in the species composition of tuna schools in the Gulf of Guinea between 1981 and  
548 1999, in relation with the fish aggregating device fishery. *Aquat. Living Resour.* 13(4),  
549 253–257. [https://doi.org/10.1016/S0990-7440\(00\)01054-8](https://doi.org/10.1016/S0990-7440(00)01054-8).
- 550 Freedman, H.I., Waltman, D., 1977. Mathematical models of population interactions with  
551 dispersal. I. Stability of two habitats with and without a predator. *SIAM J. Appl. Math.*  
552 32, 631–648. <https://doi.org/10.1137/0132052>.
- 553 Fretwell, S.D., Lucas, H.L., 1970. On territorial behaviour and other factors influenc-  
554 ing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* 19, 16-36.  
555 <https://doi.org/10.1007/BF01601953>.
- 556 Hilborn, R., Michel, F., De Leo, G.A., 2006. Integrating marine protected areas with catch  
557 regulation. *Can. J. Fish. Aquat. Sci.* 63(3), 642–649. <https://doi.org/10.1139/f05-243>.
- 558 Holt, R.T., 1985. Population Dynamics in Two-Patch Environments: Some Anoma-  
559 lous Consequences of an Optimal Habitat. *Theor. Pop. Biol.* 28, 181-208.  
560 [https://doi.org/10.1016/0040-5809\(85\)90027-9](https://doi.org/10.1016/0040-5809(85)90027-9).
- 561 Iannelli, M., Pugliese, A., 2014. *An Introduction to Mathematical Population Dynamics.*  
562 Along the trail of Volterra and Lotka. Springer.
- 563 Poggiale, J.-C., Auger, P., Nérini, D., Manté, C., Gilbert, F., 2005. Global production  
564 increased by spatial heterogeneity in a population dynamics model, *Acta Biotheor.* 53,  
565 359-370. <https://doi.org/10.1007/s10441-005-4890-3>.
- 566 Polovina, J.J., Sakai, I., 1989. Impacts of artificial reefs on fishery production in Shima-  
567 maki, Japan. *Bull. Mar. Sci.* 44, 997–1003.

- 568 Schaefer, M.B., 1957. Some considerations of population dynamics and economics in rela-  
569 tion to the management of the commercial marine fisheries. *J. Fish. Res. Board Canada*.  
570 14(5), 669-681. <https://doi.org/10.1139/f57-025>.
- 571 Smith, H.L., Thieme , H.R., 2011. *Dynamical Systems and Population Persistence*. Amer-  
572 ican Mathematical Society.
- 573 Zhang, B., DeAngelis, D.L., Ni, W.-M., 2021. Carrying Capacity of Spa-  
574 tially Distributed Metapopulations. *Trends Ecol. Evol.* 36(2), 164-173.  
575 <https://doi.org/10.1016/j.tree.2020.10.007>.
- 576 Zhang, B., Kula, A., Mack, K.M.L., Zhai, L., Ryce, A.L., Ni, W.-M., DeAngelis, D.L.,  
577 Van Dyken, J.D., 2017. Carrying capacity in a heterogeneous environment with habitat  
578 connectivity. *Ecol. Lett.* 20(9), 1118–1128. <https://doi.org/10.1111/ele.12807>.