

THE PARADOX OF CONNECTIVITY: RAPID MIGRATION ENHANCES FISH BIOMASS BUT NOT MAXIMUM SUSTAINABLE YIELD IN GENERALIZED LOGISTIC TWO-PATCH FISHERY SYSTEM

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Classical Fishery Models

Schaefer model (1954)

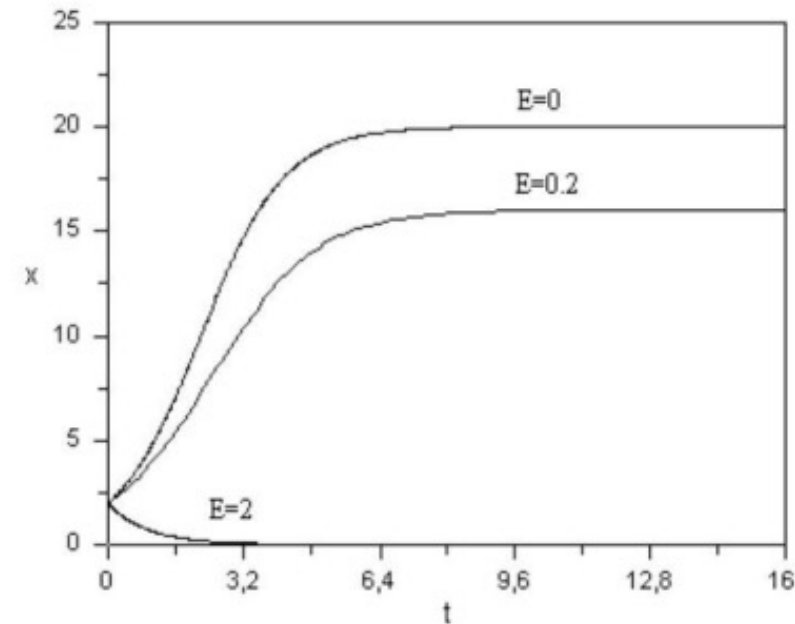
$$\frac{dn}{dt} = rn \left(1 - \frac{n}{K}\right) - qnE$$

n : biomass of fish population

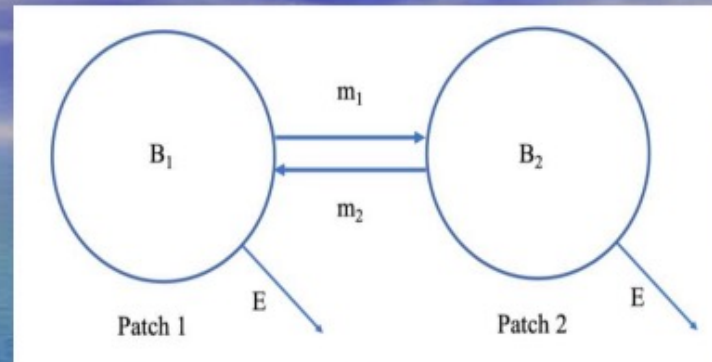
E : fishing effort

r : fish population growth rate

K : fish population carrying capacity



Two-patch Schaefer Model



Assuming fast migration, we can proceed to the reduction of the complete model :

$$\begin{aligned}\frac{dB_1}{d\tau} &= m_2 B_2 - m_1 B_1 + \epsilon \left(r_1 B_1 \left(1 - \frac{B_1}{K_1} \right) - q E B_1 \right) \\ \frac{dB_2}{d\tau} &= m_1 B_1 - m_2 B_2 + \epsilon \left(r_2 B_2 \left(1 - \frac{B_2}{K_2} \right) - q E B_2 \right)\end{aligned}$$



$$\frac{dB}{dt} = rB \left(1 - \frac{B}{K} \right) - qBE$$

Fast migration equilibrium :

$$\begin{aligned}B_1^* &= uB = \frac{m_2}{m_1 + m_2} B \\ B_2^* &= (1 - u)B = \frac{m_1}{m_1 + m_2} B\end{aligned}$$

Relationships between local and global parameters

$$\frac{dB}{dt} = rB \left(1 - \frac{B}{K} \right) - qBE$$

Global growth rate

$$r = ur_1 + (1 - u)r_2$$

with

$$u = \frac{m_2}{m_1 + m_2}$$

Global carrying capacity

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

$$K > K_1 + K_2$$

$$K_1 = K_2 = 50, r_1 = 10, r_2 = 1 \text{ and } u = \frac{1}{3} \text{ then, } K = 128.57$$

Increase in total carrying capacity in a system of two coupled logistic sites i.e. $K > K_1 + K_2$

Freedman & Waltman SIAM J Applied Math (1977) and Holt TPB (1985)

$$\begin{aligned} dN_1/dt &= N_1\phi_1(N_1) - \varepsilon N_1 + \varepsilon N_2, \\ dN_2/dt &= N_2\phi_2(N_2) + \varepsilon N_1 - \varepsilon N_2. \end{aligned} \quad (1)$$

Logistic growth, fast and symmetric migrations

As a concrete example, assume that the population in each patch follows a logistic growth law: $\phi_i = r_i(1 - N_i/K_i)$ (see Figs. 2A-E). For $\varepsilon \rightarrow \infty$ it can be shown (Freedman and Waltman, 1977) that

$$N_1^* = N_2^* = \frac{N_T^*}{2} = \frac{r_1 + r_2}{r_1/K_1 + r_2/K_2},$$

and that the change in total population size from zero dispersal is

$$K_1 + K_2 - N_T^* = \frac{(K_1 - K_2)(r_2 K_1 - r_1 K_2)}{r_1 K_1 + r_2 K_2}$$

Heterogeneous environment: K can be larger than K_1+K_2

Same carrying capacities, $K_1=K_2$, but different growth rates :

Thus, if $r_1 \neq r_2$ then there exists u_1 such that $K > 2K_1$. Moreover, the range of the parameter u_1 for which this inequality holds increases with $|r_1 - r_2|$. As a consequence, even if, in the heterogeneous case, we can have $K < 2K_1$, this inequality becomes rare in the case of strong heterogeneity. Since we are considering the case $r_1 \neq r_2$, let us assume that $r_1 > r_2$ (the opposite case would be completely similar). Then, we get:

$$u_1^+ = \frac{1}{2} \quad \text{and} \quad u_1^- = \frac{r_2}{r_1 + r_2}$$

It follows that the total carrying capacity is larger than the sum of the local carrying capacities if and only if we have the following inequalities:

$$\frac{r_2}{r_1 + r_2} < u_1 = \frac{m_{12}}{m_{12} + m_{21}} < \frac{1}{2}$$

which is equivalent to:

$$1 < \frac{m_{21}}{m_{12}} < \frac{r_1}{r_2}$$

Poggiale et al. Acta Biotheor (2005)

Arditi et al. (2015) TPB

Elbetch and Moussaoui (2023) JMB

Elbetch et al. (2020) DCDS B

De Angelis et al. (2016) JMB

De Angelis et al. (2014) DCDS B

De Angelis et al. (2015) JMB

Zhang et al. (2015) MB

Zhang et al. Ecology Letters (2017)

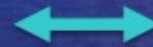
Can MSY be increased in the Two-Site Schaefer Model ?

$$\begin{aligned}\frac{dB_1}{dt} &= m_2 B_2 - m_1 B_1 + \epsilon \left(r_1 B_1 \left(1 - \frac{B_1}{K_1} \right) - q E B_1 \right) \\ \frac{dB_2}{dt} &= m_1 B_1 - m_2 B_2 + \epsilon \left(r_2 B_2 \left(1 - \frac{B_2}{K_2} \right) - q E B_2 \right)\end{aligned}$$

$$\frac{rK}{4} > \frac{r_1 K_1}{4} + \frac{r_2 K_2}{4}$$

NO ! it can be shown that the catch at MSY for connected patches is always smaller (or equal) than the sum of yields at MSY of isolated patches

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



$$(K_2 u - K_1 (1 - u))^2 \geq 0$$

using

$$r = ur_1 + (1 - u)r_2$$

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

$$K_1 = K_2 = 50, r_1 = 10, r_2 = 1 \text{ and } u = \frac{1}{3} \text{ then, } K = 128.57$$

In the previous example, even if $K > K_1 + K_2$, we have:
 $r = r_1 u + r_2 (1 - u) = 4$, $rK/4 = 128.57$, $r_1 K_1/4 + r_2 K_2/4 = 137.5$

SINGLE PATCH GENERALIZED LOGISTIC MODEL

The dynamics of the system is described by the following differential equation

$$\frac{dB}{dt} = rB \left(1 - \left(\frac{B}{K} \right)^m \right) - qEB$$

B: biomass

K: carrying Capacity

r: growth rate

q: catchability coefficient

E: fishing effort

m: generalizes the growth function

When $m = 1$, this equation reduces to the well- known classical logistic growth model.



AT EQUILIBRIUM

The biomass is given by

$$B^* = K \left(1 - \frac{qE}{r}\right)^{\frac{1}{m}}$$

The catch is

$$Y^* = qEB^* = qEK \left(1 - \frac{qE}{r}\right)^{\frac{1}{m}}$$

The catch has a maximum when $\frac{dY^*}{dE} = 0$ corresponding to the MSY when:

$$E_{MSY}^* = \frac{rm}{q(m+1)}$$

The maximum sustainable yield now reads

$$Y_{MSY}^* = \frac{m}{(m+1)^{\frac{m+1}{m}}} rK$$



TWO-PATCH GENERALIZED LOGISTIC MODEL

Migratory processes are assumed to operate on a fast time scale τ , leading to the following dynamic equations:

$$\begin{cases} \frac{dB_1}{d\tau} = n_2 B_2 - n_1 B_1 + \epsilon \left(r_1 B_1 \left(1 - \left(\frac{B_1}{K_1} \right)^m \right) - q E_1 B_1 \right) \\ \frac{dB_2}{d\tau} = n_1 B_1 - n_2 B_2 + \epsilon \left(r_2 B_2 \left(1 - \left(\frac{B_2}{K_2} \right)^m \right) - q E_2 B_2 \right) \end{cases}$$

$u_1 = \frac{n_2}{n_1 + n_2}$ and $B = B_1 + B_2$ represents the total biomass.

The fishing effort E is distributed between patches such that $E_i = v_i E$.

By substituting this fast migration equilibrium into the original system and subsequently rescaling time via $t = \epsilon \tau$

We derive the following aggregated model, which describes the system's dynamics on the slow time scale



TWO-PATCH GENERALIZED LOGISTIC MODEL

Assuming the fast migration, we can have the reduction model:

$$\frac{dB}{dt} = rB \left(1 - \left(\frac{B}{\tilde{K}} \right)^m \right) - \tilde{q}EB$$

Overall fishing effort:

$$r = r_1u_1 + r_2u_2$$

Overall fish carrying capacity:

$$\tilde{K} = \left(\alpha_1 \left(\frac{u_1}{K_1} \right)^m + \alpha_2 \left(\frac{u_2}{K_2} \right)^m \right)^{-\frac{1}{m}} \quad \text{with} \quad \alpha_1 = \frac{r_1u_1}{r} \quad \text{and} \quad \alpha_2 = \frac{r_2u_2}{r}$$

The global fishing efficiency:

$$\tilde{q} = q(u_1v_1 + u_2v_2).$$



AT EQUILIBRIUM

The biomass is given by

$$B^* = \tilde{K} \left(1 - \frac{\tilde{q}E}{r} \right)^{\frac{1}{m}}$$

The catch is

$$Y^* = \tilde{q}E\tilde{K} \left(1 - \frac{\tilde{q}E}{r} \right)^{\frac{1}{m}}$$

The catch has maximum when:

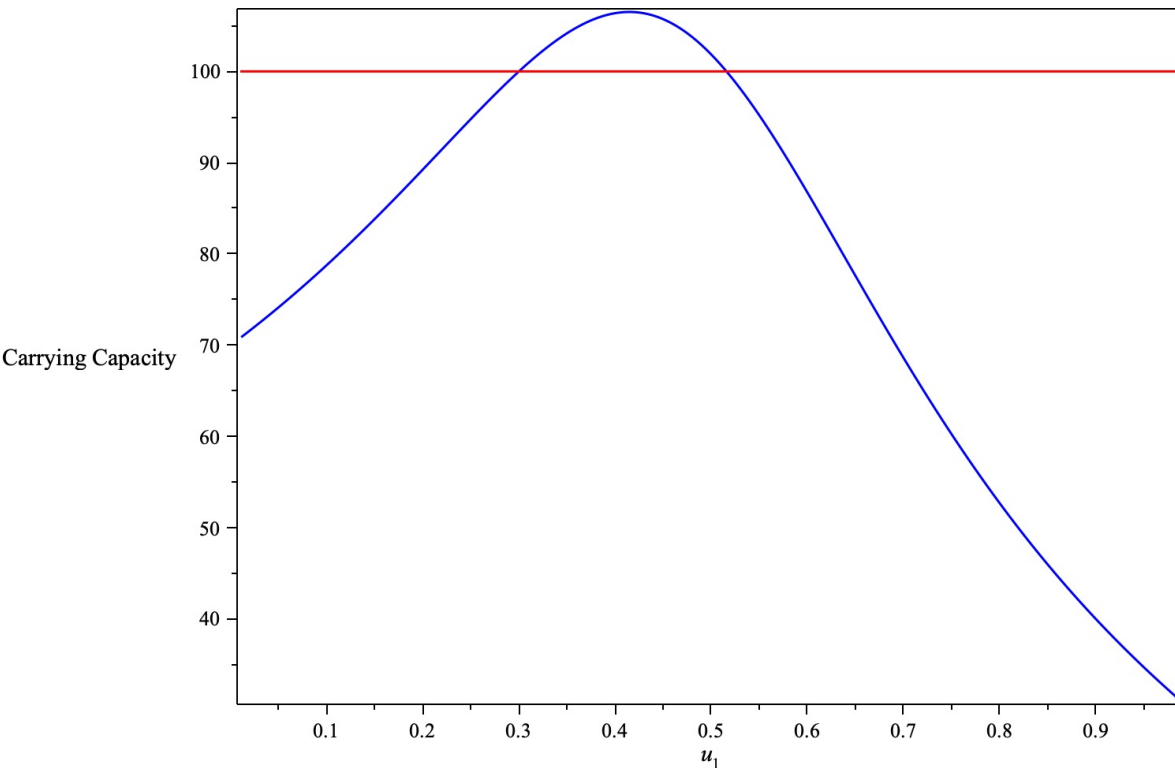
$$E_{MSY}^* = \frac{rm}{\tilde{q}(m+1)}$$

The maximum sustainable yield:

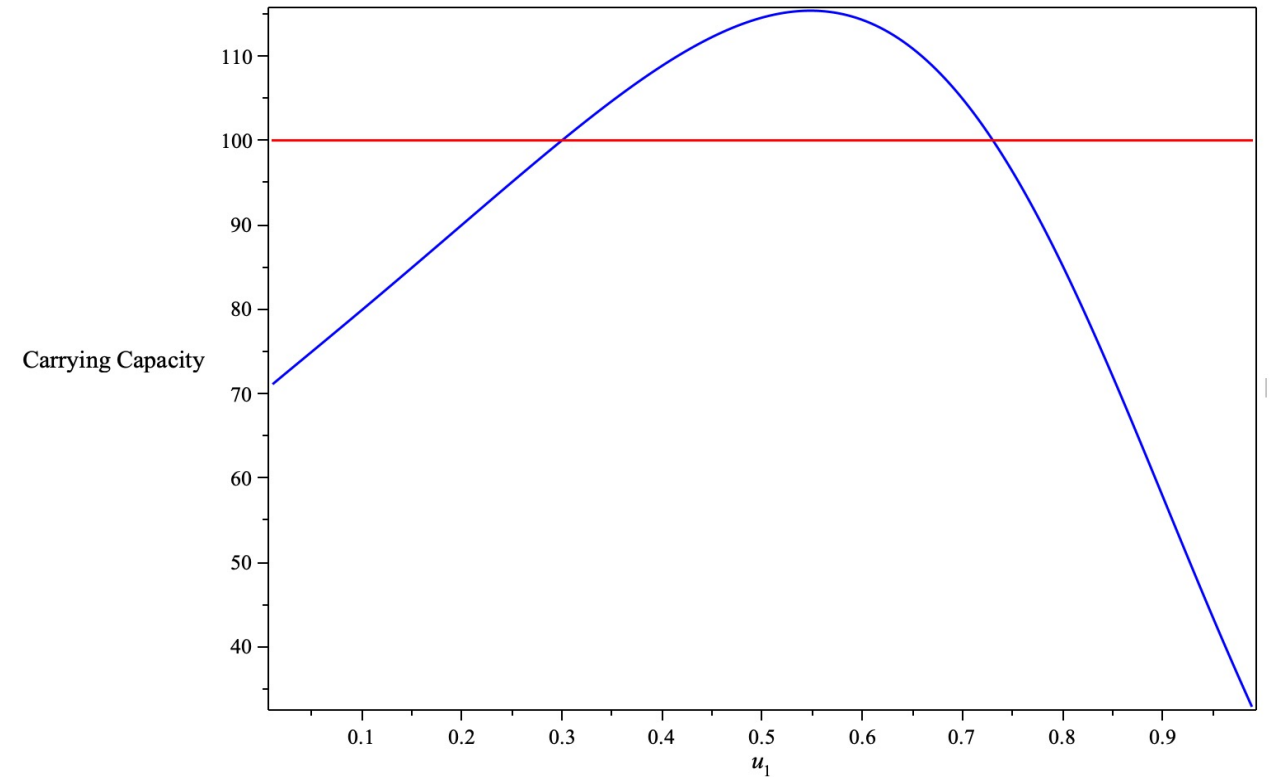
$$Y_{MSY}^* = \frac{m}{(m+1)^{\frac{m+1}{m}}} r \tilde{K}$$



COMPARING CARRYING CAPACITY



The global carrying capacity when connected (in blue) and the sum of local carrying capacities (in red) with respect to u_1 . The parameters are as follows $r_1 = 0.2$, $r_2 = 0.8$, $K_1 = 30$, $K_2 = 70$, $m = 2$



The global carrying capacity when connected (in blue) and the sum of local carrying capacities (in red) with respect to u_1 . The parameters are as follows $r_1 = 0.2$, $r_2 = 0.8$, $K_1 = 30$, $K_2 = 70$, $m = 0.5$



COMPARING MAXIMUM SUSTAINABLE YIELDS

We define the excess yield at MSY

$$\Delta Y_{MSY}^* = \frac{m}{(m+1)^{\frac{m+1}{m}}} \left(r \left(\alpha_1 \left(\frac{u_1}{K_1} \right)^m + \alpha_2 \left(\frac{u_2}{K_2} \right)^m \right)^{-\frac{1}{m}} - r_1 K_1 - r_2 K_2 \right)$$

Theorem 1. *The excess yield at MSY is non-positive i.e., $\Delta Y_{MSY}^* \leq 0$.*

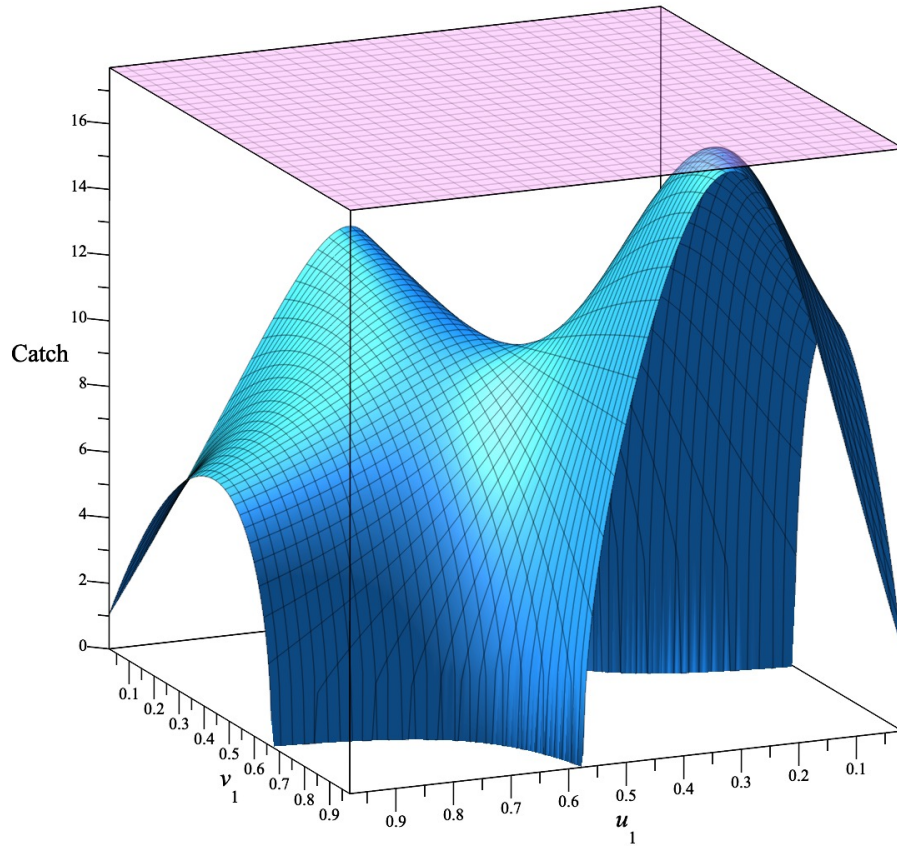
Equality holds when the fish population adheres to an Ideal Free Distribution (IFD), specifically when the per capita biomass is equal across patches

$$\left(\frac{u_1}{K_1} = \frac{u_2}{K_2} \text{ or precisely } u_1 = \frac{K_1}{K_1 + K_2} \text{ and } u_2 = \frac{K_2}{K_1 + K_2} \right)$$

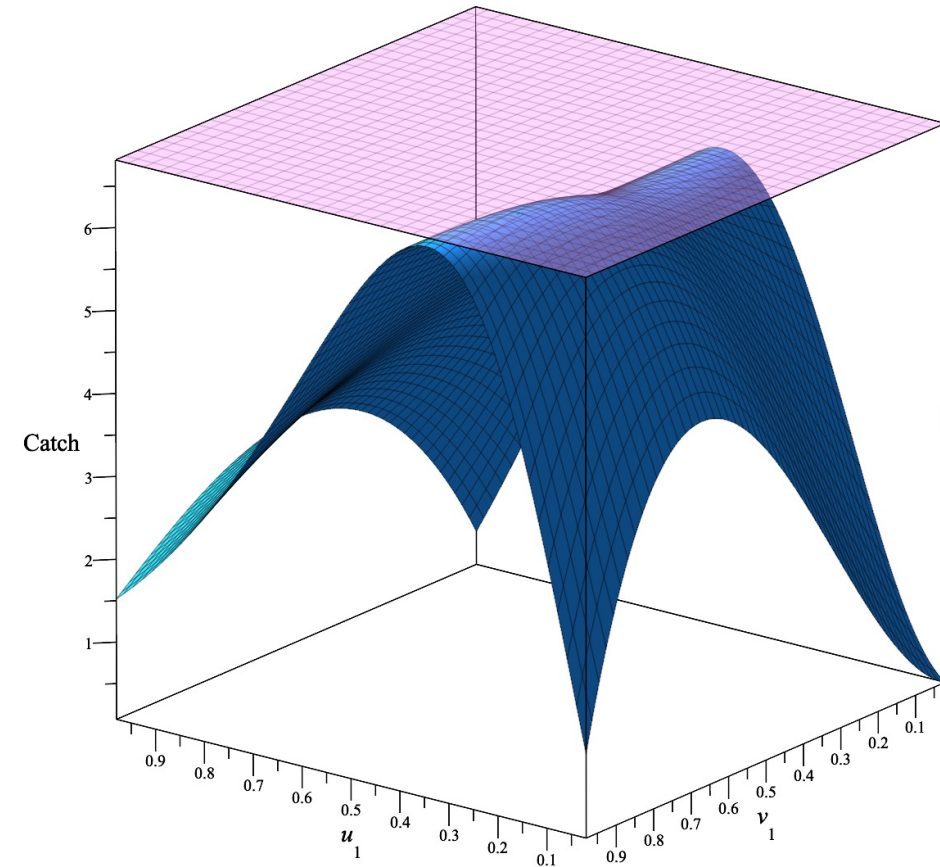
$$\tilde{K} = \tilde{K}_1 + \tilde{K}_2.$$



SIMULATIONS



Global catch (in blue) at connected patches with respect to u_1 and v_1 . The sum of the catches at MSY of the disconnected patches is represented by the violet plane and is always larger than the global catch for connected sites, with the equality holding at IFD. The parameters are given by: $r_1 = 0.6$, $r_2 = 0.4$, $K_1 = 30$, $K_2 = 70$, $q = 1$, $E = 0.9$, $m = 2$.



Global catch (in blue) at connected patches with respect to u_1 and v_1 . The sum of the catches at MSY of the disconnected patches is represented by the violet plane and is always larger than the global catch for connected sites, with the equality holding at IFD. The parameters are given by: $r_1 = 0.6$, $r_2 = 0.4$, $K_1 = 30$, $K_2 = 70$, $q = 1$, $E = 0.4$, $m = 0.5$.



THANK YOU VERY MUCH FOR YOUR ATTENTION !

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