

PNAS



1

2 **Supplementary Information for** 3 **Marine reserves promote cycles in fish populations on** 4 **ecological and evolutionary time scales**

5 **Renfei Chen¹, P. Catalina Chaparro-Pedraza¹, Suping Xiao, Pu Jia, Quan-Xing Liu², and André M. de**
6 **Roos**

7 ¹R.C. and P. C.C.-P. contributed equally to this work.

8 ²To whom correspondence should be addressed. E-mail: qx.liu@sjtu.edu.cn (Q.X.L)

9 **This PDF file includes:**

10 Supplementary text
11 Figs. S1 to S7

12 Supporting Information Text

13 Contents

14 [A Non-dimensionalization of population dynamics under fisheries strategies with reserves](#) 2

15 [B Scaling time, food and population abundance](#) 5

16 **A. Non-dimensionalization of population dynamics under fisheries strategies with reserves**

17 The life history of individual fish, determined by their growth rate g_i ($i = N, H, M$), fecundity b_i ($i = H, M$),
18 their natural mortality (μ_N and μ_G for the nursery and the growth habitat) and the fishing mortality (μ_H)
19 caused by harvesting, determine the fish population dynamics in different habitats ($i = N$ for the nursery
20 habitat occupied by smaller juveniles, $i = H$ for the harvested area in the growth habitat occupied by larger
21 juveniles and adult individuals, $i = M$ for the marine reserve in the growth habitat). The population is
22 characterised by 3 density functions $n_i(t, s)$ in the different habitat parts ($i = N, H, M$) that depend on the
23 (unscaled) fish individual body size s and time t . The dynamics of these density functions are given by:

$$24 \quad \frac{\partial n_N(t, s)}{\partial t} + g_N(F_N) \frac{\partial n_N(t, s)}{\partial s} = -\mu_N n_N(t, s) \quad [\text{A.1}]$$

$$25 \quad \frac{\partial n_H(t, s)}{\partial t} + g_H(F_H) \frac{\partial n_H(t, s)}{\partial s} = -(\mu_G + \mu_H) n_H(t, s) \quad [\text{A.2}]$$

$$26 \quad \frac{\partial n_M(t, s)}{\partial t} + g_M(F_M) \frac{\partial n_M(t, s)}{\partial s} = -\mu_G n_M(t, s) \quad [\text{A.3}]$$

29 As discussed in the main text, fish individuals born in the nursery habitat with body size (s_b) will switch
30 to the growth habitat once their body size reaches the threshold value (s_s). Therefore, the number of fish
31 individuals which reach the threshold value (s_s) in the nursery habitat equals the sum of fish individuals
32 that switched to both harvested and marine area in the growth habitat. By allocating fish individuals that
33 switch proportional to the size of the two areas in the growth habitat, we have

$$34 \quad g_H(F_H) n_H(t, s_s) = (1 - c) g_N(F_N) n_N(t, s_s) \quad [\text{A.4}]$$

$$35 \quad g_M(F_M) n_M(t, s_s) = c g_N(F_N) n_N(t, s_s) \quad [\text{A.5}]$$

37 After reaching maturity at the threshold body size s_m , adult fish individuals from the marine reserve
38 and the harvested area in the growth habitat go back to the nursery habitat to reproduce. Thus, we have

$$39 \quad g_N(F_N) n_N(t, s_b) = b(F_H) \int_{s_m}^{\infty} n_H(t, s) ds + b(F_M) \int_{s_m}^{\infty} n_M(t, s) ds \quad [\text{A.6}]$$

Eqs. A.4-A.6 represent the corresponding unscaled boundary conditions of fish population dynamics shown in Eqs. A.1-A.3. Given that fish individuals are born at body size s_b and mature at body size s_m , the total number of fish individuals are

$$\int_{s_b}^{s_s} n_N(t, s) ds$$

in the nursery habitat,

$$\int_{s_s}^{\infty} n_H(t, s) ds$$

in the harvested area of the growth habitat, and

$$\int_{s_s}^{\infty} n_M(t, s) ds$$

in the marine reserve. Correspondingly, the total fish biomass in the three different areas are

$$\int_{s_b}^{s_s} s n_N(t, s) ds$$

in the nursery habitat,

$$\int_{s_s}^{\infty} s n_H(t, s) ds$$

in the harvested area of the growth habitat and

$$\int_{s_s}^{\infty} s n_M(t, s) ds$$

in the marine reserve. As discussed in the main text, in the absence of any foraging on food resources, the dynamics of the food resource density in the nursery habitat (F_N), in the harvested area (F_H) and the marine reserve (F_M) in the growth habitat are given by

$$\frac{dF_i}{dt} = D_i - \theta F_i, \quad i = N, H, M$$

40 Including the foraging by fish, the dynamics of the food resource densities are given by:

$$41 \quad \frac{dF_N}{dt} = D_N - \theta F_N - a_N F_N \int_{s_b}^{s_s} n_N(t, s) ds \quad [A.7]$$

$$42 \quad \frac{dF_H}{dt} = D_H - \theta F_H - a_H F_H \int_{s_s}^{\infty} n_H(t, s) ds \quad [A.8]$$

$$44 \quad \frac{dF_M}{dt} = D_M - \theta F_M - a_M F_M \int_{s_s}^{\infty} n_M(t, s) ds \quad [A.9]$$

To non-dimensionalize the model, we define

$$w = \frac{s - s_b}{s_m - s_b}$$

and

$$w_s = \frac{s_s - s_b}{s_m - s_b}$$

Thus, the density functions $n_N(t, s)$, $n_H(t, s)$ and $n_M(t, s)$ can be rescaled to density functions $m_N(t, w)$, $m_H(t, w)$ and $m_M(t, w)$ by the following transformation:

$$m_i(t, w) = (s_m - s_b)n_i(t, s_b + (s_m - s_b)w), \quad i = N, H, M$$

These transformations lead to the following identity:

$$\begin{aligned} \int_{w_1}^{w_2} m_i(t, w)dw &= \int_{w_1}^{w_2} (s_m - s_b)n_i(t, s_b + (s_m - s_b)w)d\left(\frac{s - s_b}{s_m - s_b}\right) \\ &= \int_{s_b + (s_m - s_b)w_1}^{s_b + (s_m - s_b)w_2} n_i(t, s)ds \end{aligned}$$

46 Using these identities we can derive the PDEs for $m_N(t, w)$:

$$\begin{aligned} \frac{\partial m_N(t, w)}{\partial t} &= (s_m - s_b) \frac{\partial n_N(t, s_b + (s_m - s_b)w)}{\partial t} \\ &= -(s_m - s_b)g_N(F_N) \frac{\partial n_N(t, s_b + (s_m - s_b)w)}{\partial s} - \mu_N m_N(t, w) \\ 47 &= -g_N(F_N) \frac{\partial m_N\left(t, \frac{s - s_b}{s_m - s_b}\right)}{\partial s} - \mu_N m_N(t, w) \\ &= -\frac{g_N(F_N)}{s_m - s_b} \frac{\partial m_N(t, w)}{\partial w} - \mu_N m_N(t, w) \end{aligned}$$

48 and similarly for $m_H(t, w)$ and $m_M(t, w)$:

$$\begin{aligned} \frac{\partial m_H(t, w)}{\partial t} &= -\frac{g_H(F_H)}{s_m - s_b} \frac{\partial m_H(t, w)}{\partial w} - (\mu_G + \mu_H)m_H(t, w) \\ 49 & \\ \frac{\partial m_M(t, w)}{\partial t} &= -\frac{g_M(F_M)}{s_m - s_b} \frac{\partial m_M(t, w)}{\partial w} - \mu_G m_M(t, w) \end{aligned}$$

50 Defining

$$\tilde{g}_N(F_N) = \frac{\epsilon_g}{s_m - s_b} a_N F_N$$

51
$$\tilde{g}_H(F_H) = \frac{\epsilon_g}{s_m - s_b} a_H F_H$$

$$\tilde{g}_M(F_M) = \frac{\epsilon_g}{s_m - s_b} a_M F_M$$

52 the rescaled model equations for the dynamics of the food resource densities in the nursery habitat, the
53 harvested area and the marine reserve in the growth habitat are then given by

54
$$\frac{dF_N}{dt} = D_N - \theta F_N - a_N F_N \int_0^{w_s} m_N(t, w) dw \quad [\text{A.10}]$$

55
$$\frac{dF_H}{dt} = D_H - \theta F_H - \frac{a_H F_H}{1 - c} \int_{w_s}^{\infty} m_H(t, w) dw \quad [\text{A.11}]$$

56
$$\frac{dF_M}{dt} = D_M - \theta F_M - \frac{a_M F_M}{c} \int_{w_s}^{\infty} m_M(t, w) dw \quad [\text{A.12}]$$

57 and the dynamics of the size-dependent density functions of the fish population are given by:

58
$$\begin{cases} \frac{\partial m_N(t, w)}{\partial t} + \tilde{g}_N(F_N) \frac{\partial m_N(t, w)}{\partial w} = -\mu_N m_N(t, w) \\ \tilde{g}_N(F_N) m_N(t, 0) = b(F_H) \int_1^{\infty} m_H(t, w) dw + b(F_M) \int_1^{\infty} m_M(t, w) dw \end{cases} \quad [\text{A.13}]$$

59
$$\begin{cases} \frac{\partial m_H(t, w)}{\partial t} + \tilde{g}_H(F_H) \frac{\partial m_H(t, w)}{\partial w} = -(\mu_G + \mu_H) m_H(t, w) \\ \tilde{g}_H(F_H) m_H(t, w_s) = (1 - c) \tilde{g}_N(F_N) m_N(t, w_s) \end{cases} \quad [\text{A.14}]$$

60
$$\begin{cases} \frac{\partial m_M(t, w)}{\partial t} + \tilde{g}_M(F_M) \frac{\partial m_M(t, w)}{\partial w} = -\mu_G m_M(t, w) \\ \tilde{g}_M(F_M) m_M(t, w_s) = c \tilde{g}_N(F_N) m_N(t, w_s) \end{cases} \quad [\text{A.15}]$$

61 B. Scaling time, food and population abundance

Define the following scaled variables:

$$t' = t/t^*$$

$$F'_N = F_N/F_N^*$$

$$F'_H = F_H/F_H^*$$

$$F'_M = F_M/F_M^*$$

$$m'_N(t, w) = m_N(t, w)/m^*$$

$$m'_H(t, w) = m_H(t, w)/m^*$$

$$m'_M(t, w) = m_M(t, w)/m^*$$

62 Substituting these in the model equations yields:

$$\frac{dF'_N}{dt'} = \frac{t^*}{F_N^*} D_N - t^* \theta F'_N - t^* a_N F'_N m^* \int_0^{w_s} m'_N(t, w) dw$$

63
$$\frac{dF'_H}{dt'} = \frac{t^*}{F_H^*} D_H - t^* \theta F'_H - t^* \frac{a_H F'_H}{1-c} m^* \int_{w_s}^{\infty} m'_H(t, w) dw$$

$$\frac{dF'_M}{dt'} = \frac{t^*}{F_M^*} D_M - t^* \theta F'_M - t^* \frac{a_M F'_M}{c} m^* \int_{w_s}^{\infty} m'_M(t, w) dw$$

64
$$\begin{cases} \frac{\partial m'_N(t, w)}{\partial t'} = -t^* \tilde{g}_N(F_N) \frac{\partial m'_N(t, w)}{\partial w} - t^* \mu_N m'_N(t, w) \\ t^* \tilde{g}_N(F_N) m'_N(t, 0) = t^* b(F_H) \int_1^{\infty} m'_H(t, w) dw + t^* b(F_M) \int_1^{\infty} m'_M(t, w) dw \end{cases} \quad [\text{A.16}]$$

65
$$\begin{cases} \frac{\partial m'_H(t, w)}{\partial t'} = -t^* \tilde{g}_H(F_H) \frac{\partial m'_H(t, w)}{\partial w} - t^* (\mu_G + \mu_H) m'_H(t, w) \\ t^* \tilde{g}_H(F_H) m'_H(t, w_s) = (1-c) t^* \tilde{g}_N(F_N) m'_N(t, w_s) \end{cases} \quad [\text{A.17}]$$

66
$$\begin{cases} \frac{\partial m'_M(t, w)}{\partial t'} = -t^* \tilde{g}_M(F_M) \frac{\partial m'_M(t, w)}{\partial w} - t^* \mu_G m'_M(t, w) \\ t^* \tilde{g}_M(F_M) m'_M(t, w_s) = t^* c \tilde{g}_N(F_N) m'_N(t, w_s) \end{cases} \quad [\text{A.18}]$$

where

$$t^* \tilde{g}_i(F_i) = t^* F_i^* \frac{\epsilon_g}{s_m - s_b} a_i F'_i$$

and

$$t^* b(F_H) = t^* F_H^* \epsilon_b a_H F'_H, \quad t^* b(F_M) = t^* F_M^* \epsilon_b a_M F'_M.$$

Choosing the scaling such that

$$\frac{t^*}{F_N^*} = \frac{t^*}{F_H^*} = \frac{t^*}{F_M^*} = \frac{1}{D_N} \implies F_N^* = F_H^* = F_M^* = D_N t^*$$

$$t^* m^* = \frac{1}{a_N} \implies m^* = \frac{1}{a_N t^*}$$

$$t^* F_N^* = t^* F_H^* = t^* F_M^* = \frac{s_m - s_b}{\epsilon_g a_N}$$

Then

$$D_N(t^*)^2 = \frac{s_m - s_b}{\epsilon_g a_N}$$

67 and hence

$$68 \quad t^* = \sqrt{\frac{s_m - s_b}{\epsilon_g a_N D_N}} \quad [\text{A.19}]$$

$$69 \quad F_N^* = F_H^* = F_M^* = \sqrt{\frac{(s_m - s_b) D_N}{\epsilon_g a_N}} \quad [\text{A.20}]$$

$$70 \quad m^* = \sqrt{\frac{\epsilon_g D_N}{(s_m - s_b) a_N}} \quad [\text{A.21}]$$

71 The rescaled model is:

$$72 \quad \frac{dF'_N}{dt'} = 1 - \theta \sqrt{\frac{s_m - s_b}{\epsilon_g a_N D_N}} F'_N - F'_N \int_0^{w_s} m'_N(t, w) dw$$

$$73 \quad \frac{dF'_H}{dt'} = \frac{D_H}{D_N} - \theta \sqrt{\frac{s_m - s_b}{\epsilon_g a_N D_N}} F'_H - \frac{a_H/a_N F'_H}{1-c} \int_{w_s}^{\infty} m'_H(t, w) dw$$

$$74 \quad \frac{dF'_M}{dt'} = \frac{D_M}{D_N} - \theta \sqrt{\frac{s_m - s_b}{\epsilon_g a_N D_N}} F'_M - \frac{a_M/a_N F'_M}{c} \int_{w_s}^{\infty} m'_M(t, w) dw$$

$$75 \quad \begin{cases} \frac{\partial m'_N(t, w)}{\partial t'} = -F'_N \frac{\partial m'_N(t, w)}{\partial w} - \mu_N \sqrt{\frac{s_m - s_b}{\epsilon_g a_N D_N}} m'_N(t, w) \\ F'_N m'_N(t, 0) = \frac{(s_m - s_b) \epsilon_b}{\epsilon_g} \frac{a_H}{a_N} F'_H \int_1^{\infty} m'_H(t, w) dw + \frac{(s_m - s_b) \epsilon_b}{\epsilon_g} \frac{a_M}{a_N} F'_M \int_1^{\infty} m'_M(t, w) dw \end{cases}$$

$$76 \quad \begin{cases} \frac{\partial m'_H(t, w)}{\partial t'} = -\frac{a_H}{a_N} F'_H \frac{\partial m'_H(t, w)}{\partial w} - (\mu_G + \mu_H) \sqrt{\frac{s_m - s_b}{\epsilon_g a_N D_N}} m'_H(t, w) \\ \frac{a_H}{a_N} F'_H m'_H(t, w_s) = (1-c) \frac{a_M}{a_N} F'_M m'_M(t, w_s) \end{cases}$$

$$77 \quad \begin{cases} \frac{\partial m'_M(t, w)}{\partial t'} = -\frac{a_M}{a_N} F'_M \frac{\partial m'_M(t, w)}{\partial w} - \mu_G \sqrt{\frac{s_m - s_b}{\epsilon_g a_N D_N}} m'_M(t, w) \\ \frac{a_M}{a_N} F'_M m'_M(t, w_s) = c F'_N m'_N(t, w_s) \end{cases}$$

78 Defining scaled parameters as in Table 1 (see Methods), $\gamma_N(F_N) = F_N$, $\gamma_H(F_H) = q_H F_H$ and $\gamma_M(F_M)$

79 $= q_M F_M$, substitution in the model equations yields:

$$80 \quad \frac{dF_N}{dt} = 1 - \delta F_N - \int_0^{w_s} \gamma_N(F_N) m_N(t, w) dw \quad [\text{A.22}]$$

$$81 \quad \frac{dF_H}{dt} = \rho_H - \delta F_H - \frac{1}{1-c} \int_{w_s}^{\infty} \gamma_H(F_H) m_H(t, w) dw \quad [\text{A.23}]$$

$$82 \quad \frac{dF_M}{dt} = \rho_M - \delta F_M - \frac{1}{c} \int_{w_s}^{\infty} \gamma_M(F_M) m_M(t, w) dw \quad [\text{A.24}]$$

$$83 \quad \begin{cases} \frac{\partial m_N(t, w)}{\partial t} + \gamma_N(F_N) \frac{\partial m_N(t, w)}{\partial w} = -\eta_N m_N(t, w) \\ \gamma_N(F_N) m_N(t, 0) = \beta \gamma_H(F_H) \int_N^{\infty} m_H(t, w) dw + \beta \gamma_M(F_M) \int_N^{\infty} m_M(t, w) dw \end{cases} \quad [\text{A.25}]$$

$$84 \quad \begin{cases} \frac{\partial m_H(t, w)}{\partial t} + \gamma_H(F_H) \frac{\partial m_H(t, w)}{\partial w} = -(\eta_G + \eta_H) m_H(t, w) \\ \gamma_H(F_H) m_H(t, w_s) = (1-c) \gamma_N(F_N) m_N(t, w_s) \end{cases} \quad [\text{A.26}]$$

$$85 \quad \begin{cases} \frac{\partial m_M(t, w)}{\partial t} + \gamma_M(F_M) \frac{\partial m_M(t, w)}{\partial w} = -\eta_G m_M(t, w) \\ \gamma_M(F_M) m_M(t, w_s) = c \gamma_N(F_N) m_N(t, w_s) \end{cases} \quad [\text{A.27}]$$

86 In this rescaled model, equations [A.22](#), [A.23](#), and [A.24](#) describe the dynamics of the food resource
87 density in the nursery habitat, in the harvested area of the growth habitat, and in the marine reserve.
88 Equations [A.25](#), [A.26](#) and [A.27](#) describe the dynamic of the size-dependent density functions of the
89 population, including the boundary conditions at the scaled birth size $w = 0$ in the nursery habitat (in
90 eq. [A.25](#)), and at the switching size $w = w_s$ from the nursery habitat to the harvested area in the growth
91 habitat (in eq. [A.26](#)) and the marine reserve (in eq. [A.27](#)).

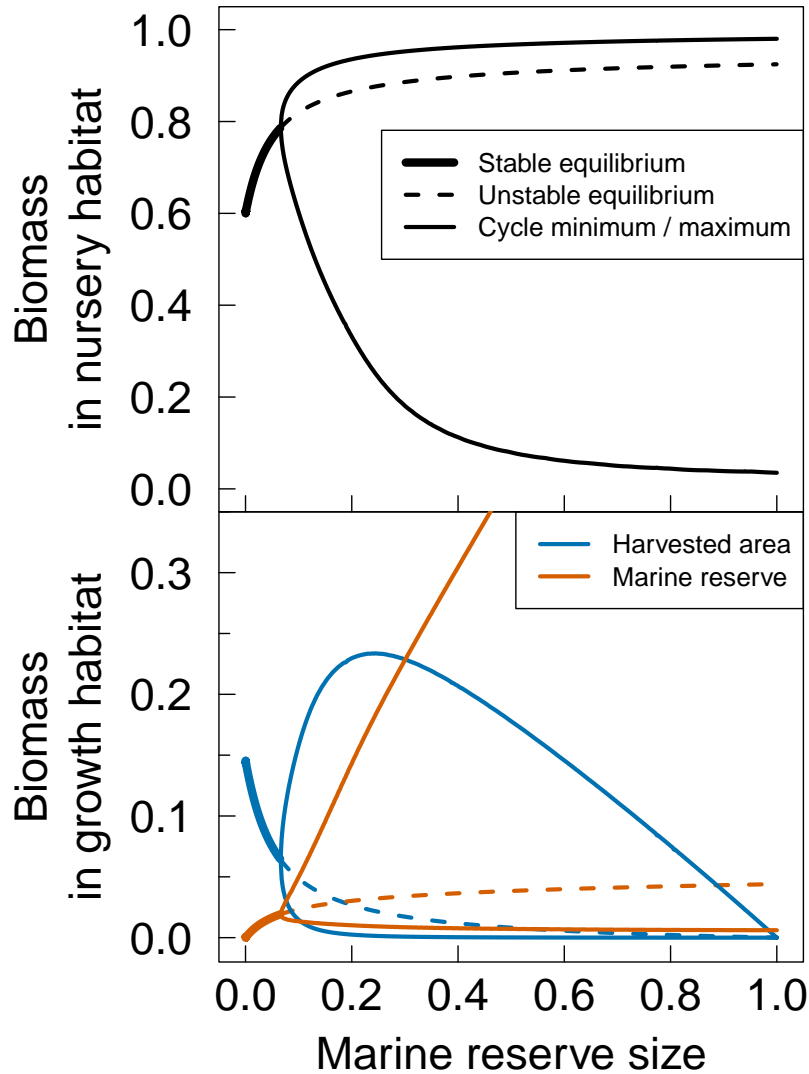


Fig. S1. Equilibrium states and maximum and minimum values occurring during population oscillations of total fish biomass in the nursery habitat (*top*), and in the harvested area and the marine reserve (*bottom*) as a function of the marine reserve size. Thick solid lines represent stable equilibrium states, thin solid lines represent maximum and minimum values during population oscillations. Dashed lines represent unstable equilibrium states. See Methods for calculation details. Parameter values as in Table 1 in the main text.

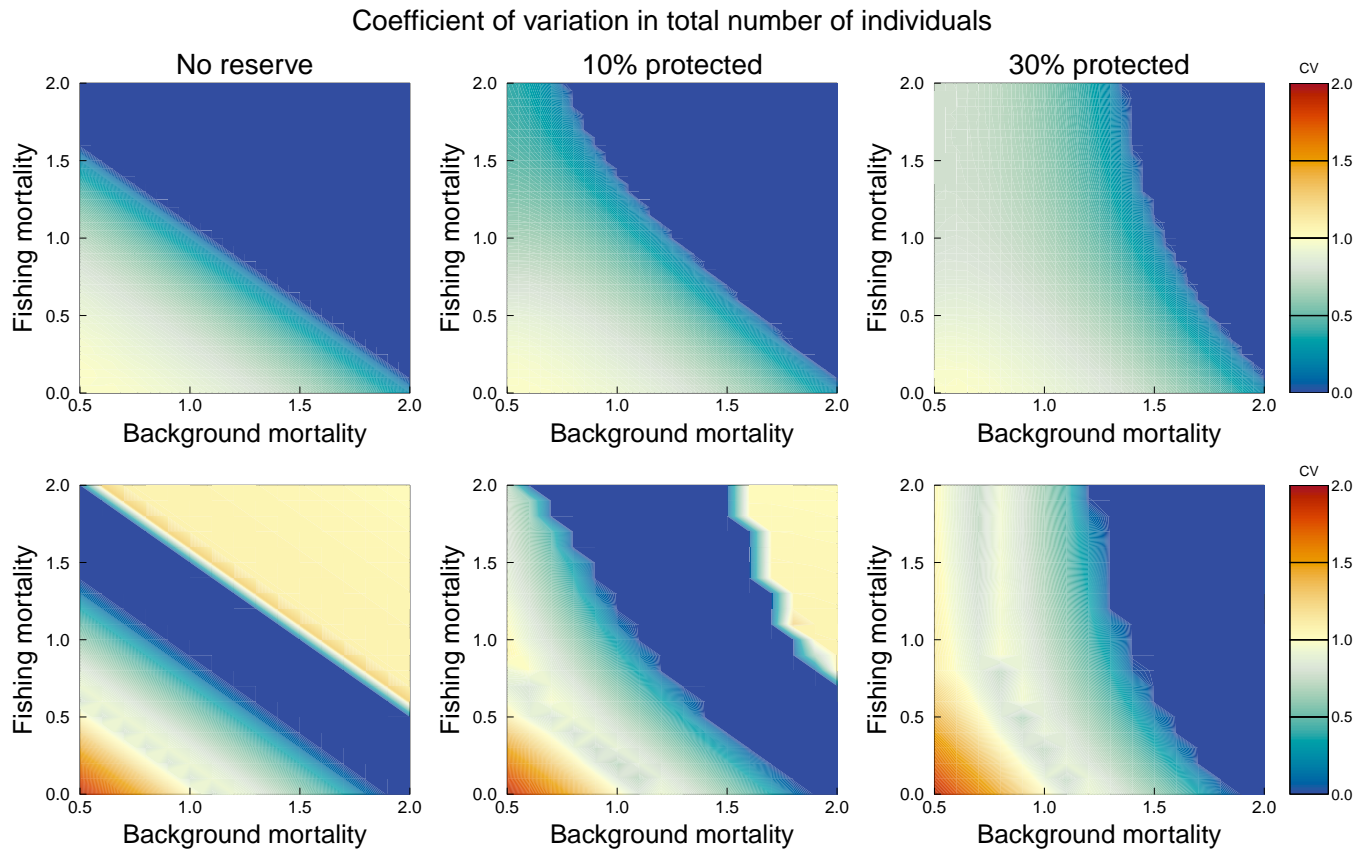


Fig. S2. Heatmaps showing the coefficient of variation of the total number of individuals in the population during ecological dynamics without evolutionary change in the body size at habitat shift w_s (*top row*; with $w_s = 0.374$, corresponding to the evolutionary stable value in the absence of a marine reserve; see Fig. 4 in main text) and when the body size at habitat shift evolves over time (*bottom row*) for different values of the background mortality in the harvested area and the marine reserve (parameter n_G) and the fishing mortality in the harvested area (parameter n_H) in the absence of a marine reserve (*left*) and when the marine reserve covers 10% and 30% of the growth habitat (*middle* and *right* panels, respectively). Other parameter values as given in Table 1 in the main text.

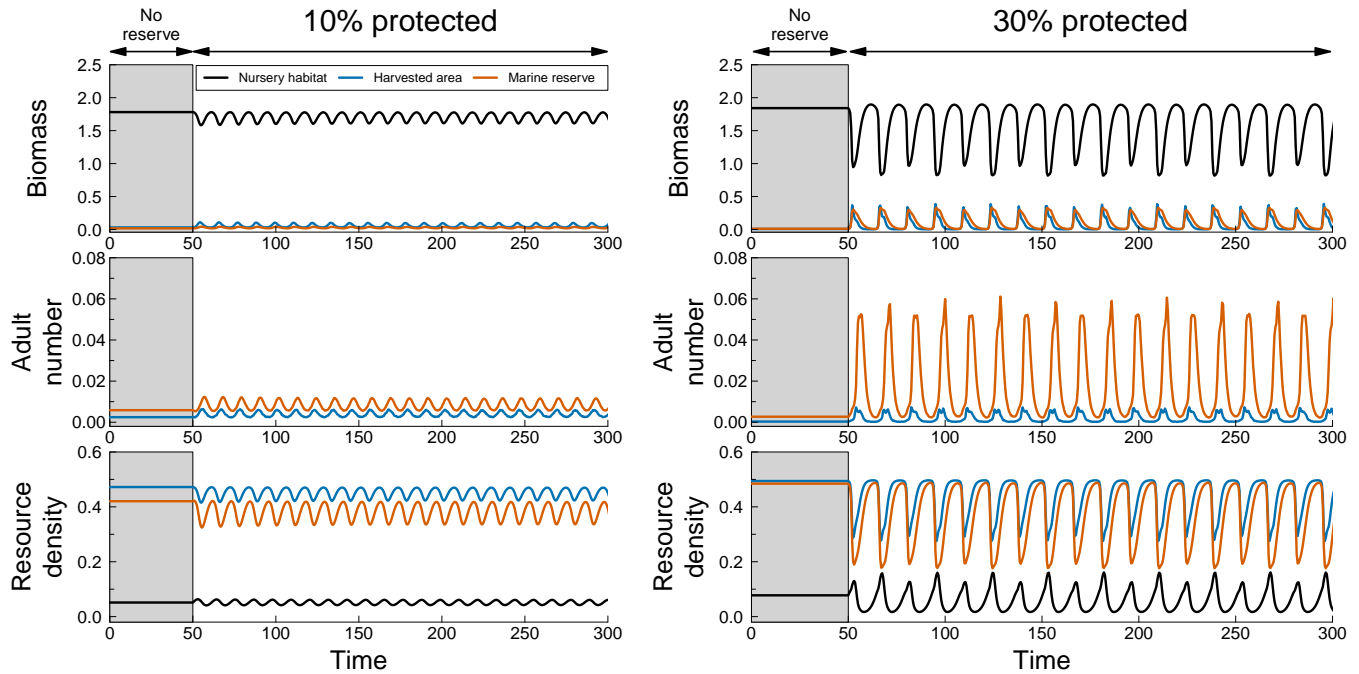


Fig. S3. Ecological dynamics of total fish biomass (*top*), adult density (*middle*) and resource density (*bottom*) in the nursery habitat, the harvested area and the marine reserve following the establishment of a marine reserve at $t = 50$ (the reserve does not exist yet during the time interval in grey, $t = 0 - 50$), when the marine reserve covers 10% (*left*, $c = 0.1$) or 30% (*right*, $c = 0.3$) of the growth habitat. Evolutionary change in the body size at habitat shift does not occur, which is constant at $w_s = 0.374$, corresponding to the evolutionary stable value in the absence of a marine reserve (see Fig. 4 in main text). Mortality rate in nursery habitat equal to $\eta_N = 0.5$ (compare with Fig. 4 in main text where $\eta_N = 1.0$), other parameter values as given in Table 1 in the main text.

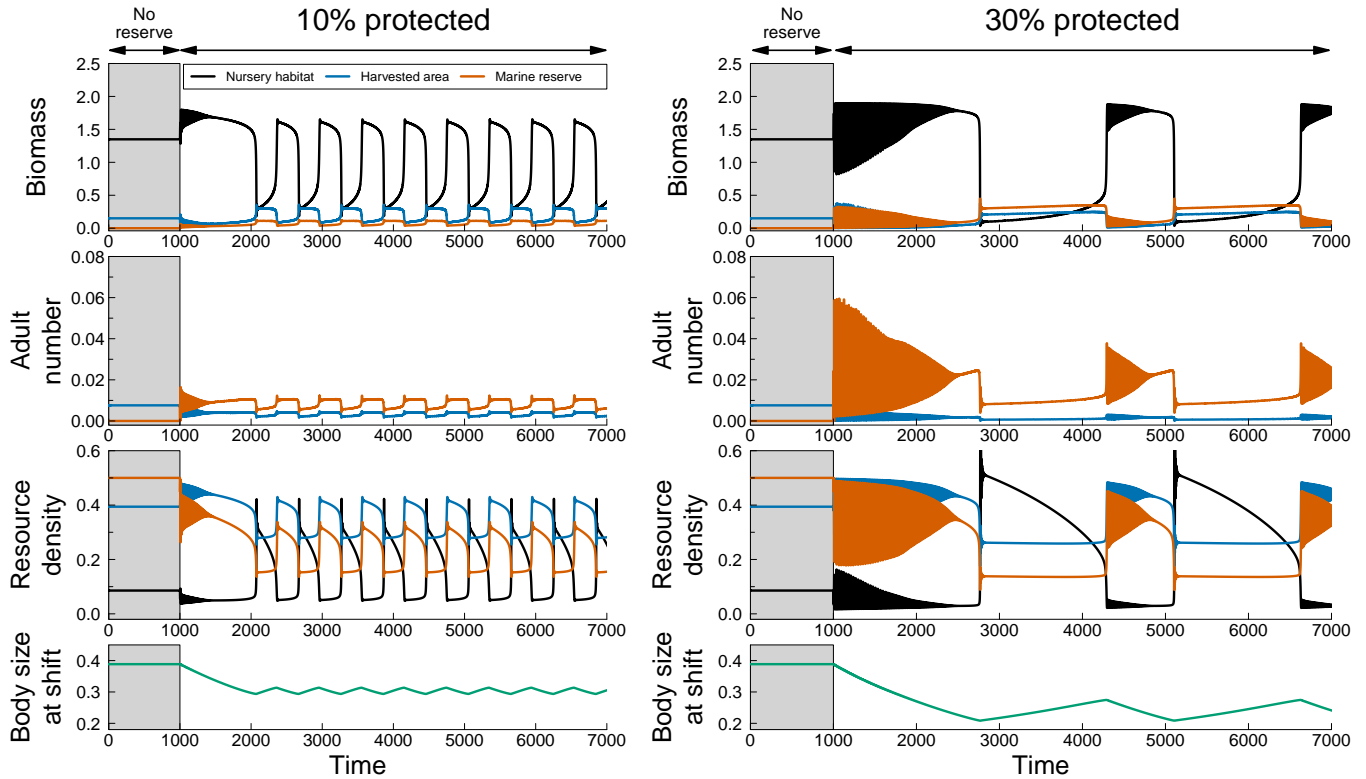


Fig. S4. Eco-evolutionary dynamics of total fish biomass (*top row*), adult density (*2nd row*) and resource density (*3rd row*) in the nursery habitat, the harvested area and the marine reserve and the body size at habitat shift (*bottom row*) following the establishment of a marine reserve at $t = 1000$ (reserve does not exist yet during the time interval in grey, $t = 0 - 1000$), when the body size at habitat shift evolves over time and the marine reserve covers 10% (*left*, $c = 0.1$) or 30% (*right*, $c = 0.3$) of the growth habitat. Notice that the ecological cycles with a period of approximately 10 time units that are visible in Fig. S3 show up in this figure as solidly colored areas with decreasing amplitude over time. Mortality rate in nursery habitat equal to $\eta_N = 0.5$ (compare with Fig. 4 in main text where $\eta_N = 1.0$), other parameter values as given in Table 1 in the main text.

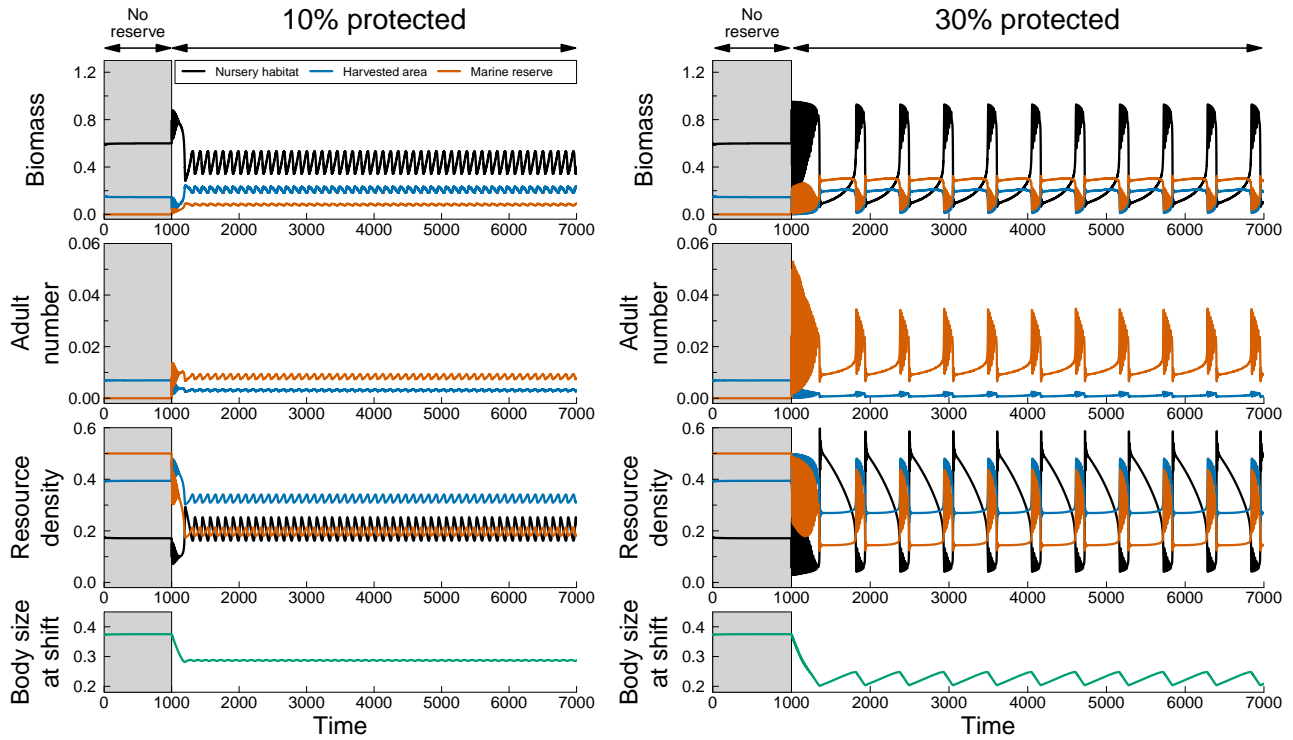


Fig. S5. Eco-evolutionary dynamics of total biomass, the number of adult individuals and the resource density in the nursery habitat, the harvested area and the marine reserve and the body size at habitat shift in case of large genetic variance ($2\sigma = 0.4$) before (time interval in grey, $t = 0 - 1000$) and after the establishment of a marine reserve ($t = 1000 - 7000$). Comparison of dynamics with changing values of marine reserve size (*Left*: $c = 0.1$; *Right*: $c = 0.3$). Parameter values given in Table 1 in the main text. Compare with Fig. 3 in the main text.

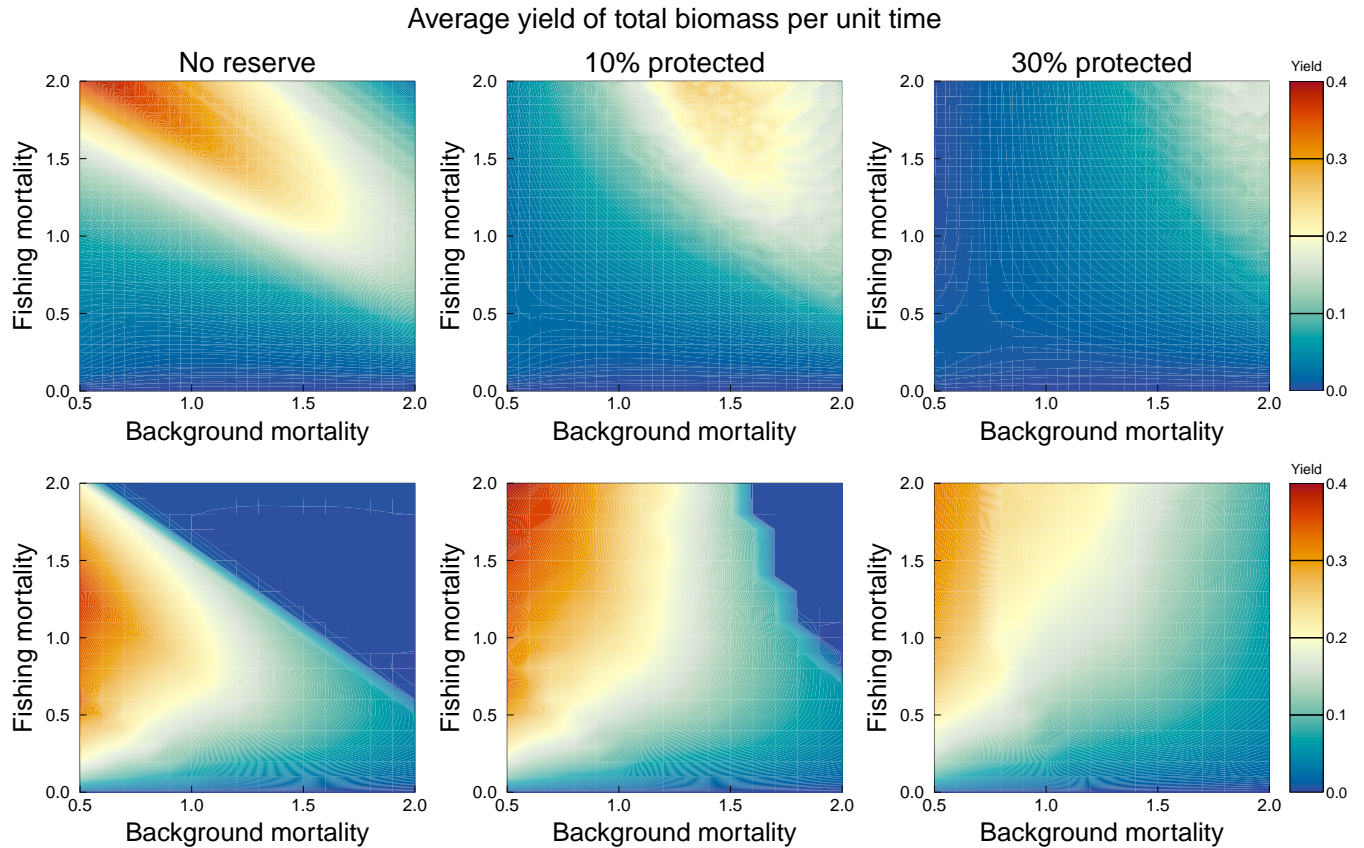


Fig. S6. Heatmaps showing the average yield per unit time in terms of total biomass during ecological dynamics without evolutionary change in the body size at habitat shift w_s (*top row*; with $w_s = 0.374$, corresponding to the evolutionary stable value in the absence of a marine reserve; see Fig. 4 in main text) and when the body size at habitat shift evolves over time (*bottom row*) for different values of the background mortality in the harvested area and the marine reserve (parameter n_G) and the fishing mortality in the harvested area (parameter n_H) in the absence of a marine reserve (*left*) and when the marine reserve covers 10% and 30% of the growth habitat (*middle* and *right* panels, respectively). Other parameter values as given in Table 1 in the main text.

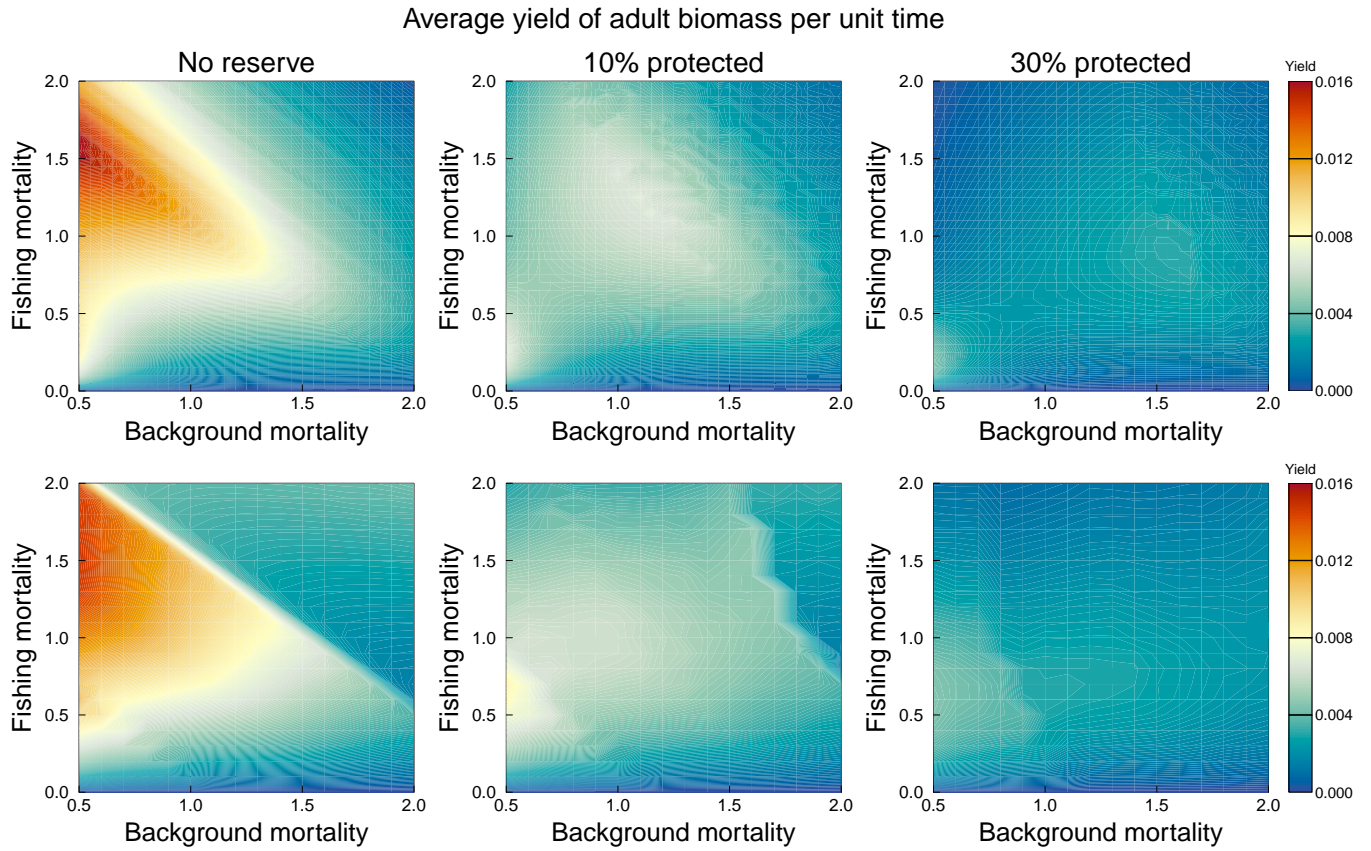


Fig. S7. Heatmaps showing the average yield per unit time in terms of adult biomass only during ecological dynamics without evolutionary change in the body size at habitat shift w_s (*top row*; with $w_s = 0.374$, corresponding to the evolutionary stable value in the absence of a marine reserve; see Fig. 4 in main text) and when the body size at habitat shift evolves over time (*bottom row*) for different values of the background mortality in the harvested area and the marine reserve (parameter n_G) and the fishing mortality in the harvested area (parameter n_H) in the absence of a marine reserve (*left*) and when the marine reserve covers 10% and 30% of the growth habitat (*middle* and *right* panels, respectively). Other parameter values as given in Table 1 in the main text.