

MULTISPECIES EXPLOITATION WITH EVOLUTIONARY SWITCHING OF HARVESTING STRATEGIES

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ABSTRACT. In this paper, we propose a bioeconomic model which describes a fishery in which each of two noninteracting species is harvested by a given group of fishers during a defined time period. Then the Fishing Regulatory Authority allows each fisher to reconsider the harvesting decision at fixed (discrete) periods of time. The model derives from an Italian fisheries management experience in the Northern Adriatic Sea, where this kind of “self-adjusting” fishing policy has been proposed to regulate harvesting of two shellfish species. The proposed dynamic model assumes the form of a hybrid system, as the natural growth functions of the two species (in continuous time) are coupled with a discrete time adaptive system that regulates how agents switch from one harvesting strategy to the other period by period according to an evolutionary mechanism based on profit comparison. In order to obtain some insights into the basic mechanisms of the system, some relevant benchmark cases are analyzed before tackling (mainly numerically) the complete hybrid model. Our results suggest that, for proper sets of parameters, this kind of myopic and adaptive self-regulation may ensure a virtuous trade-off between profit maximization and resource conservation, driven by cost externalities and market pressure.

KEY WORDS: Fisheries management, mathematical bioeconomics, heterogeneous agents, evolutionary game theory, hybrid dynamical systems.

1. Introduction. In order to avoid the overexploitation of some fisheries, management institutions usually enforce forms of regulation, either by imposing harvesting restrictions, such as constant efforts, individual fishing quotas, taxation, etc., or by limiting the kinds of fish to be caught or the regions where exploitation is allowed (see e.g., Clark [1990], Fischer and Mirman [1992], Fischer and Mirman [1996], Anderson [2002], Bischi and Lamantia [2009], Bischi et al. [2009b]). Usually, optimal policies are established by solving suitable long-run optimization problems,

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for instance estimating the maximum sustainable yield (MSY) for fisheries and assessing the relative social impact. Any miscomputation of the total catch can easily lead the resource to the verge of collapse. Moreover, fishers have to accept the adopted fishing restriction and there is the problem of controlling compliance to the prescribed catch. To make things more complicated, the strategic interaction between fishers usually gives an incentive to free-ride and overexploit to single agents, according to the well-known problem of the “tragedy of the commons” (see Hardin [1968]), as documented by empirical fisheries data in McWhinnie [2009].

However, even economic externalities may have an indirect impact on harvesting pressure and can be employed in regulation. For instance, increasing harvesting (and thus quantity of the resource on the market) usually leads to price reductions and so to lower profits. Similarly cost externalities come into play, as stock depletion leads to increments of landing costs and so again to lower profits. Some experiments on endogenous regulatory policies of common pool resources have been recently performed on the basis of these self-regulating economic externalities. In particular, fishing institutions only establish general rules, and then fishers are allowed to decide fishing strategies on their own. Along these lines, it is more reasonable to assume that exploiters decide their catches in order to maximize their short-term profit instead of solving optimal control problems. In fact, the long-run sustainability of exploitation is more an objective for the farsighted regulator, whereas it is more likely that fishers behave myopically.

For example, a recent law proposed in Italy to regulate the harvesting of two noninteracting shellfishes (*Venerupis aurea* and *Callista chione*) in the Adriatic Sea, requires that each agent can harvest only one species in any three-year period, possibly revising his/her choice in predefined successive periods, but no limits on individual quotas are set. In other words, instead of imposing a difficult-to-control policy (e.g., imposed effort, total allowable catch, etc.), the fishing institution only establishes that each vessel can harvest just one species in each period and has to stick to this choice for a given time interval. In the revision of their strategy, agents compare their average profits with the ones obtained by the agents who made a different choice over the last fishing period. These average profits are taken as a proxy of the fitness of a strategy, according to the paradigms of evolutionary game theory (see Weibull [1995], Hofbauer and Sigmund [1998]).

The aim of the paper is to use analytical and numerical methods to analyze the economic consequences of this kind of self-regulating fishery, as well as to shed some light on the sustainability of this form of exploitation in comparison to other policies. Indeed, our analysis gives evidence of possible advantages of profit-driven self-regulated harvesting strategy choices over other practices, both from the point of view of biomass levels (i.e., biological sustainability) and wealth (economic profitability). Moreover, the simulation results suggest that this kind of myopic evolutionary regulation in certain cases can ensure a virtuous trade-off between profit maximization and resource conservation.

We develop a standard model for each of two species, then allow fishers to switch between the two fisheries at prespecified time periods. We consider four management strategies: (1) unrestricted harvesting; (2) splitting the fishers between the two fisheries equally; (3) allowing the fishers to choose continuously; and (4) only allowing switching at prespecified periods. Case 4 gives rise to a hybrid dynamic model, which is the nearest to a real-world application but quite difficult to study analytically, so the other cases mainly serve as benchmarks. Even if far from the real system we want to describe, particularly cases 2 and 3 can give useful suggestions about the directions of investigation of the more realistic hybrid system, as well as some intuitive interpretations of the properties observed through numerical simulations.

The structure of the paper is as follows. The bioeconomic model is introduced in Section 2, where agents' harvesting functions are defined under various assumptions about fishing restrictions. Section 3 defines the switching mechanism exploiters employ to decide the species to harvest from period to period. The main properties of the model with switching in continuous time are also studied in this section. Some numerical simulations are proposed in Section 4 in order to understand peculiar features of the proposed hybrid system. Section 5 concludes that allowing switching between separate fisheries may have a long-term positive effect on stocks and profits under certain conditions.

2. The bioeconomic models. Let us consider a simple marine ecosystem with two noninteracting species, indexed by 1 and 2, each with its own habitat, and biomass (or density) measures X_1 and X_2 , respectively, both subject to commercial harvesting. We assume that their time evolution is described by a dynamical system of the form:

$$(1) \quad \begin{aligned} \dot{X}_1 &= X_1 G_1(X_1) - H_1(X_1, X_2) \\ \dot{X}_2 &= X_2 G_2(X_2) - H_2(X_1, X_2), \end{aligned}$$

where \dot{X}_i denotes the derivatives of biomass with respect to time, G_i specifies the natural growth function, and H_i represents the instantaneous harvesting of species $i = 1, 2$.

According to Melià and Gatto [2005], we assume that the two populations of (shell)fish follow a logistic natural growth of the form

$$(2) \quad G_i = \rho_i \left(1 - \frac{X_i}{k_i} \right); \quad i = 1, 2,$$

where ρ_i and k_i are, respectively, the intrinsic rate of growth and the carrying capacity of species i .

These two species are harvested by N agents. We assume that H_i , the current total harvesting of species i , is wholly supplied to the market, and prices are determined according to the following horizontal differentiated linear inverse demand system (see Singh and Vives [1984], Häckner [2000]):

$$(3) \quad \begin{aligned} p_1 &= f_1(H_1, H_2) = a_1 - b_1(H_1 + \sigma H_2) \\ p_2 &= f_2(H_1, H_2) = a_2 - b_2(\sigma H_1 + H_2), \end{aligned}$$

where a_i is the reservation price for species i , b_i represents the slope of the demand for fish i and $\sigma \in [0, 1]$ is the symmetric degree of substitutability between the two fish varieties. In particular, if $\sigma = 0$ then the two varieties are independent in demand. On the other hand, for $\sigma = 1$ they are perfect substitutes.¹ In addition, we also assume quadratic harvesting costs for both species, i.e., for harvesting h_i units of species i an agent incurs a cost given by

$$(4) \quad C_i(X_i, h_i) = \gamma_i \frac{h_i^2}{X_i},$$

where γ_i is the cost parameter for catching species i . This cost function is obtained and employed in Clark [1990] and Szidarovszki and Okuguchi [1998] and used by several authors (see e.g., Conrad and Smith [2012]). As shown in the Appendix, equation (4) can be derived from a Cobb–Douglas type “production function” with fishing effort (labor) and fish biomass (capital) as production inputs. This production function exhibits decreasing marginal returns to both input factors: for the biomass they are a consequence of gear saturation, which occurs whenever the fishing nets have a maximum capacity, whereas decreasing catch-per-unit-effort (CPUE) captures the problem of congestion among fishing vessels. In particular, the Cobb–Douglas production function is based on the assumption that gear saturation and congestion reduce the mortality rate of one unit of biomass and the CPUE in a smooth manner. Other mathematical forms of the production function can capture similar effects, as suggested in Clark [1990].

2.1. Unrestricted harvesting. Although rarely observed in real-world examples of fisheries, the case of unrestricted harvesting developed in this section serves as a benchmark case for comparison purposes. By unrestricted harvesting we mean that a generic fisher has no constraint on quantity and kind of fish to harvest. The current profit of a generic agent that harvests the quantities h_1^F and h_2^F of species 1 and 2 reads:

$$\pi^F = p_1 h_1^F + p_2 h_2^F - \gamma_1 \frac{(h_1^F)^2}{X_1} - \gamma_2 \frac{(h_2^F)^2}{X_2}.$$

If fisher q , $q = 1, \dots, N$ is allowed to catch without constraints and tries to maximize current profits, his/her problem is given by $\max_{h_{1,q}^F; h_{2,q}^F} \pi_q^F$, where

$$\begin{aligned} \pi_q^F &= \left\{ a_1 - b_1 \left[h_{1,q}^F + \sigma h_{2,q}^F + \sum_{u=1; u \neq q}^N (h_{1,u}^F + \sigma h_{2,u}^F) \right] \right\} h_{1,q}^F \\ &+ \left\{ a_2 - b_2 \left[h_{2,q}^F + \sigma h_{1,q}^F + \sum_{u=1; u \neq q}^N (h_{2,u}^F + \sigma h_{1,u}^F) \right] \right\} h_{2,q}^F \\ &- \gamma_1 \frac{(h_{1,q}^F)^2}{X_1} - \gamma_2 \frac{(h_{2,q}^F)^2}{X_2}, \end{aligned}$$

the $h_{i,q}^F$, $i = 1, 2$; $q = 1, \dots, N$, denotes the harvesting of species i by fisher q in case of unrestricted harvesting.

Instantaneous optimal harvesting can be obtained by solving the system of first-order conditions² $\frac{\partial \pi_q^F}{\partial h_{1,q}} = 0$ and $\frac{\partial \pi_q^F}{\partial h_{2,q}} = 0$. Note that, since all agents face the same optimization problem, we can solve the system of first-order conditions by letting $h_{i,q}^F = h_{i,u}^F$, $i = 1, 2$; $q, u = 1, \dots, N$. Hence, in the case of unrestricted harvesting, the equilibrium harvesting quantities $h_i^{F,*}$ by a representative player for catching species i reads

$$\begin{aligned} h_i^{F,*}(X_i, X_j) &= \\ &\frac{a_j(b_j + Nb_i)X_i X_j \sigma - a_i X_i(b_j(1 + N)X_j + 2\gamma_j)}{(b_i + Nb_j)(b_j + Nb_i)X_i X_j \sigma^2 - (b_i(1 + N)X_i + 2\gamma_i)(b_j(1 + N)X_j + 2\gamma_j)}; \\ &i, j = 1, 2; i \neq j \end{aligned}$$

In the particular case $b_1 = b_2 = b = 0$, i.e., perfectly elastic demands for both species, the individual optimal harvesting of species i and the resulting total instantaneous profit can be written in the following simplified form:

$$(5) \quad h_i^{F,*} = \frac{a_i X_i}{2\gamma_i}, \quad \pi_i^{F,*} = \sum_{i=1}^2 \frac{a_i}{2} h_i^{F,*}; \quad i = 1, 2.$$

In fisheries models, prices are often assumed to be constant as fish is considered a staple food for the majority of consumers, there are many substitutes for each species and many fish are internationally traded (see Clark [1990] and Conrad and Smith [2012]).

2.2. Restricted harvesting. In this subsection, we obtain the harvesting function under the assumption that an authority restricts each agent to catch only one species at a time. Let us assume that, in a given time period, agents are partitioned into two groups, with $m_1 = m$ agents in group 1 (harvesting species 1 only) and $m_2 = N - m$ agents in group 2 (harvesting species 2 only).

Given the specifications of cost functions and prices as above, the profit of fisher q in group i ($= 1, 2$) when harvesting $h_{i,q}$ reads

$$(6) \quad \pi_{i,q} = p_i h_{i,q} - \gamma_i \frac{h_{i,q}^2}{X_i}, \quad i = 1, 2.$$

Therefore, in deciding his/her instantaneous harvesting of species i , the representative fisher q in group i solves the problem $\max_{h_{i,q}} \pi_{i,q}$, where

$$\pi_{i,q} = \left\{ a_i - b_i \left[h_{i,q} + \sum_{u \in m_i; u \neq q} h_{i,u} + \sigma \sum_{u \in m_j} h_{j,u} \right] \right\} h_{i,q} - \gamma_i \frac{h_{i,q}^2}{X_i}; \quad i, j = 1, 2, i \neq j.$$

By taking the first-order conditions and employing the symmetry property that players within each group are homogeneous (i.e., $h_{i,q} = h_{i,u}, i = 1, 2; q, u \in m_i$), we obtain the following harvesting quantities at a Nash equilibrium

$$(7) \quad h_i^*(X_i, X_j) = \frac{a_i X_i (b_j X_j (1 + N r_j) + 2 \gamma_j) - a_j b_i N r_j X_i X_j \sigma}{(b_i X_i (1 + N r) + 2 \gamma_i) (b_j X_j (1 + N (1 - r)) + 2 \gamma_j) - b_i b_j N^2 (1 - r) r X_i X_j \sigma^2}; \quad i, j = 1, 2, i \neq j,$$

where $r_1 = r = \frac{m_1}{N}$ and $r_2 = (1 - r) = \frac{m_2}{N}$ represent, respectively, the fractions of agents in group 1 and 2.

By inserting (7) into (6), we get optimal individual profits

$$(8) \quad \pi_i^* = \left(b_i + \frac{\gamma_i}{X_i} \right) (h_i^*)^2$$

which shows that profits are non-negative. Of course, if profits are positive (or at least non-negative), then also optimal harvesting (7) is positive.

The assumption $b_1 = b_2 = b = 0$ allows us to obtain a simpler expression for individual optimal harvesting profit, which constitutes a useful benchmark in the

following:

$$(9) \quad h_i^* = \frac{a_i X_i}{2\gamma_i}, \quad \pi_i^* = \frac{a_i}{2} h_i^*; \quad i = 1, 2.$$

Although harvesting expressions in (5) and (9) are the same because there is no interaction via the demand curve, in the case of restricted harvesting each agent can not access both stocks. In fact, profits for each fisher in (5) are the sum of profits from both species, whereas in 9 profits to each agent come from the only species caught.

3. Switching mechanism. In this section we explain the basic dynamic mechanism that regulates how the fraction $r(t)$ of exploiters of species 1 (or, equivalently, the fraction $1 - r(t)$ of exploiters of species 2) is updated over time in the case of restricted harvesting. In this case, recall that an authority imposes that fishers have to stick to the decided strategy for a given period of time $s > 0$, after which they can reconsider their decisions on the basis of observed profits. This period-by-period adaptive mechanism can be described by an endogenous evolutionary dynamic, for instance through a replicator equation in discrete time (see Weibull [1995], Hofbauer and Sigmund [1998], Bischi et al. [2009a]). More specifically, let us assume that at the end of each time period of length s , a representative agent in group i assesses his/her average profit $\bar{\pi}_i^*$ over that period, given by

$$(10) \quad \bar{\pi}_i^*(t) = \frac{\int_{t-s}^t \pi_i^*(\tau) d\tau}{s}; \quad i = 1, 2.$$

If the magnitude of $\bar{\pi}_i^*(t)$ can be estimated by all agents, i.e., it is a common knowledge, it can be employed as a shared fitness measure for playing strategy i . This leads to the following dynamic model, expressed by continuous time growth and harvesting of the fish species and discrete (or pulse) fishing strategy switching (a discrete decision-driven time)³

$$(11) \quad \begin{cases} \dot{X}_1(t) = X_1(t)G_1(X_1(t)) - Nr(t)h_1^*(X_1(t), X_2(t)) \\ \dot{X}_2(t) = X_2(t)G_2(X_2(t)) - N(1 - r(t))h_2^*(X_1(t), X_2(t)) \\ r(t) = \begin{cases} \frac{r(t-s)\frac{\bar{\pi}_1^*(t)}{r(t-s)\bar{\pi}_1^*(t) + [1 - r(t-s)]\bar{\pi}_2^*(t)}}{r\left(\left\lfloor \frac{t}{s} \right\rfloor s\right)} & \text{if } \frac{t}{s} = \left\lfloor \frac{t}{s} \right\rfloor, \\ \text{otherwise} \end{cases} \end{cases}$$

where $\lfloor x \rfloor$ is the largest integer not greater than x (i.e., the floor of x), and $h_i^*(X_1(t), X_2(t))$, $\bar{\pi}_i^*(t)$, $i = 1, 2$ are given, respectively, in (7) and (10). The third equation states that at each switching time, each representative fisher is assumed

to know the average profits during the previous period both of fishers of the same group and also of fishers of the other group. If we observe $\bar{\pi}_1^*(t) > \bar{\pi}_2^*(t)$ then $r(t)$ increases, i.e., a fraction of fishers harvesting species 2 switches to harvest species 1, otherwise $r(t)$ decreases.

Given $X_1(0)$, $X_2(0)$, and $r(0)$, for each $t \geq 0$ the time evolution of $X_i(t)$, $i = 1, 2$, and $r(t)$ is thus regulated by the hybrid dynamical system (11). The term hybrid indicates that $X_1(t)$ and $X_2(t)$ evolve in continuous time, whereas $r(t)$ is updated according to a discrete time scale.

In the limiting case $s \rightarrow 0$, i.e., with fishers changing their strategy continuously (i.e., the species to harvest), $\bar{\pi}_i^*(t) = \pi_i^*(t)$ and the last equation in (11) can be replaced with

$$(12) \quad \begin{aligned} \dot{r}(t) &= r(t) [\pi_1^*(t) - (r(t)\pi_1^*(t) + (1-r(t))\pi_2^*(t))] \\ &= r(t)(1-r(t)) [\pi_1^*(t) - \pi_2^*(t)] \end{aligned}$$

which is the well-known replicator equation in continuous time (see again Weibull [1995] and Hofbauer and Sigmund [1998]), stating that $\dot{r}(t) > 0$ if $\pi_1^*(t) > \pi_2^*(t)$. In this case, the model assumes the simpler form of a nonlinear three-dimensional system of ordinary differential equations (ODEs). This simpler specification constitutes a useful benchmark. In fact, an equilibrium point for the system with continuous replicator (12) is also a fixed point for the hybrid system (11), although the converse is not necessarily true. This follows from the fact that the first and the second dynamic equations in the two specifications are identical, and the replicator dynamics in discrete time have the same equilibrium conditions: $r(t) = r(t-s)$ for $r = 0$, $r = 1$ or $\pi_1^*(t) = \pi_2^*(t)$. In fact, if instantaneous profits are identical in equilibrium, then the average profits of the two strategies over the nonswitching time interval of length s are also identical. Nonetheless, we can have an equilibrium point such that the average profits of the two strategies over the interval s are equal, even though instantaneous profits are not equal over the interval. As we shall see, in case (11), $r(t)$ becomes a piecewise-constant function, like an endogenously driven bang-bang parameter whose discontinuous jumps occur at discrete times and lead to sudden switching among different dynamic scenarios, which is typical behavior of hybrid systems (see e.g., Aubin et al. [2002], Haddad et al. [2006], Goebel et al. [2009]).

3.1. Equilibria and stability analysis with continuous switching. In order to obtain analytical results, let us consider the system (1) with replicator dynamics in continuous time (12) and constant prices (i.e., $b_1 = b_2 = 0$). The

dynamical model assumes the form of the following system of ODEs:

$$(13) \quad \begin{cases} \dot{X}_1 = X_1 \rho_1 \left(1 - \frac{X_1}{k_1} \right) - Nr \frac{a_1 X_1}{2\gamma_1} \\ \dot{X}_2 = X_2 \rho_2 \left(1 - \frac{X_2}{k_2} \right) - N(1-r) \frac{a_2 X_2}{2\gamma_2} , \\ \dot{r} = r(1-r) \left[\frac{a_1^2 X_1}{4\gamma_1} - \frac{a_2^2 X_2}{4\gamma_2} \right] \end{cases}$$

where we omitted the dependence on t , as no confusion arises. Note that in the invariant subspaces defined by $r = 0$ and 1 , the first two differential equations in (13) are uncoupled. The following propositions (proved in the Appendix) describe the steady states of the model and their local stability properties. To keep the notation short, in these propositions it is useful to define the aggregate parameters

$$(14) \quad \alpha_1(r) = \rho_1 - \frac{a_1 Nr}{2\gamma_1} \quad \text{and} \quad \alpha_2(r) = \rho_2 - \frac{a_2 N(1-r)}{2\gamma_2}.$$

Proposition 1. (*Boundary equilibria and their stability*).

For the system of ODEs (13) the following statements hold:

- (1) the total extinction fixed points $E^0 = (0, 0, r)$, where $r = [0, 1]$, are unstable non-hyperbolic nodes provided that $\alpha_i(r) > 0$, $i = 1, 2$;
- (2) the equilibria with harvesting of only one species are given by:
 - (i) $E_1^0 = (k_1, 0, 0)$ and $E_2^0 = (0, k_2, 1)$ [extinction of the harvested species], which are saddle points;
 - (ii) $E_1^1 = (0, k_2(1 - N\frac{a_2}{2\gamma_2\rho_2}), 0)$, if $Na_2 < 2\gamma_2\rho_2$, and $E_2^1 = (k_1(1 - N\frac{a_1}{2\gamma_1\rho_1}), 0, 1)$, if $Na_1 < 2\gamma_1\rho_1$ [extinction of the nonharvested species], which are saddle points;
 - (iii) $E_1^2 = (k_1, k_2(1 - N\frac{a_2}{2\gamma_2\rho_2}), 0)$ if $Na_2 < 2\gamma_2\rho_2$ [both viable species with no harvesting of species 1], which is a stable node provided that

$$(15) \quad a_1 < \sqrt{\frac{a_2^2 k_2 \gamma_1 (2\gamma_2 \rho_2 - Na_2)}{2k_1 \gamma_2^2 \rho_2}}$$

and a saddle point if the reverse inequality in (15) holds;

(iv) $E_2^2 = (k_1(1 - N \frac{a_1}{2\gamma_1\rho_1}), k_2, 1)$ if $Na_1 < 2\gamma_1\rho_1$ [both viable species with no harvesting of species 2] which is a stable node provided that

$$(16) \quad a_2 < \sqrt{\frac{a_1^2 k_1 \gamma_2 (2\gamma_1 \rho_1 - Na_1)}{2k_2 \gamma_1^2 \rho_1}}$$

and a saddle point if the reverse inequality in (16) holds.

The next proposition characterizes an equilibrium with $r^* \in (0, 1)$, which is the case in which each species is always harvested by some fishers, of course with the restriction that each agent is allowed to fish just one species.

Proposition 2. (Inner equilibrium and its stability).

For the system of ODEs (13) the following statements hold:

(i) There exists a unique inner equilibrium $E^* = (X_1^*, X_2^*, r^*)$ with $r^* \in (0, 1)$, where

$$(17) \quad \begin{aligned} X_i^* &= \frac{a_j^2 k_1 k_2 \gamma_i (2a_2 \gamma_1 \rho_1 + 2a_1 \gamma_2 \rho_2 - a_1 a_2 N)}{2(a_2^3 k_2 \gamma_1^2 \rho_1 + a_1^3 k_1 \gamma_2^2 \rho_2)}, \quad i = 1, 2; i \neq j \\ r^* &= \frac{\gamma_1 \rho_1 (a_2^3 k_2 N \gamma_1 - 2a_2^2 k_2 \gamma_1 \gamma_2 \rho_2 + 2a_1^2 k_1 \gamma_2^2 \rho_2)}{N (a_2^3 k_2 \gamma_1^2 \rho_1 + a_1^3 k_1 \gamma_2^2 \rho_2)}. \end{aligned}$$

(ii) Equilibrium biomass levels $X_i^* > 0, i = 1, 2$ iff $\alpha_i(r^*) > 0$, with $0 < r^* < 1$; this occurs in the following cases:

Case 1: If $\alpha_1(1) > 0$ and $\alpha_2(0) > 0$ then the carrying capacity k_1 must satisfy

$$\widehat{k}_1 = \frac{a_2^2 k_2 \gamma_1 (2\gamma_2 \rho_2 - Na_2)}{2a_1^2 \gamma_2^2 \rho_2} < k_1 < \frac{2a_2^2 k_2^2 \gamma_1^2 \rho_1}{2a_1^2 \gamma_1 \gamma_2 \rho_1 - Na_1^3 \gamma_2} = \bar{k}_1;$$

Case 2: If $\alpha_1(1) > 0$ and $\alpha_2(0) < 0$ then the carrying capacity k_1 must satisfy $0 < k_1 < \bar{k}_1$;

Case 3: If $\alpha_1(1) < 0$ and $\alpha_2(0) > 0$ then the carrying capacity k_1 must satisfy $k_1 > \bar{k}_1$;

Case 4: If $\alpha_1(1) < 0$ and $\alpha_2(0) < 0$ then it must be $\frac{2\gamma_1\rho_1}{N} < a_1 < \frac{2a_2\gamma_1\rho_1}{Na_2 - 2\gamma_2\rho_2}$, and at $a_1 = \frac{2a_2\gamma_1\rho_1}{Na_2 - 2\gamma_2\rho_2}$ it is $X_1^* = X_2^* = 0$;

Case 5: Finally, if $k_1 = \bar{k}_1$ then it is $r^* = 0$ and $E^* = E_1^2 = (k_1, k_2(1 - N \frac{a_2}{2\gamma_2\rho_2}), 0)$ whereas if $k_1 = \bar{k}_1$ then it is $r^* = 1$ and $E^* = E_2^2 = (k_1(1 - N \frac{a_1}{2\gamma_1\rho_1}), k_2, 1)$.

(iii) If the equilibrium $E^* = (X_1^*, X_2^*, r^*)$ involves positive biomasses, then it is stable under the replicator dynamics in continuous time.

The cases discussed in the previous proposition help to understand through which contacts (with border equilibria) the inner equilibrium appears or disappears. In particular, the last two cases indicate that the inner equilibrium can have a contact with extinction equilibrium E^0 or with the border equilibria E_1^2 and E_2^2 .

It is also interesting to notice that, by Proposition 1, a single species, say species 1, does not become extinct provided that $\frac{2\gamma_1\rho_1}{a_1N} > r$, whereas by Proposition 2, the condition $r^* < 1$ leads to $\frac{2\gamma_1\rho_1}{a_1N} < 1 + \frac{2a_2^2k_2\gamma_1^2\rho_1}{Na_1^3k_1\gamma_2}$. Therefore, if

$$(18) \quad \frac{2\gamma_1\rho_1}{a_1N} \in \left(r, 1 + \frac{2a_2^2k_2\gamma_1^2\rho_1}{Na_1^3k_1\gamma_2} \right)$$

then species 1 will survive both with an exogenous fixed r or with a r^* to which the continuous time switching mechanism converges. However, if the fixed $r = \bar{r} \in (0, 1)$ is such that

$$(19) \quad \frac{2\gamma_1\rho_1}{a_1N} \in (0, r),$$

i.e., too much harvesting pressure is imposed on species 1, then this fixed \bar{r} will lead the resource to extinction, whereas an endogenous r could avoid the occurrence of extinction for species 1 (the same reasoning applies, of course, to species 2).

For the sake of comparison, the analytical results on the coexistence of both species can be synthesized as follows:

Corollary 1. *If $k_1, k_2 > 0$ and $\frac{2\rho_1\gamma_1}{Na_1} + \frac{2\rho_2\gamma_2}{Na_2} > 1$, the model with continuous replicator dynamics (13) converges to one of the following fixed points with coexistence of the two species:*

- E_1^2 if $\frac{2\gamma_2\rho_2}{a_2N} \in \left(1 + \frac{2a_1^2k_1\gamma_2^2\rho_2}{Na_2^3k_2\gamma_1}, +\infty \right)$;
- E_2^2 if $\frac{2\gamma_1\rho_1}{a_1N} \in \left(1 + \frac{2a_2^2k_2\gamma_1^2\rho_1}{Na_1^3k_1\gamma_2}, +\infty \right)$;
- E^* whenever $\frac{2\gamma_1\rho_1}{a_1N} < 1 + \frac{2a_2^2k_2\gamma_1^2\rho_1}{Na_1^3k_1\gamma_2}$ and $\frac{2\gamma_2\rho_2}{a_2N} < 1 + \frac{2a_1^2k_1\gamma_2^2\rho_2}{Na_2^3k_2\gamma_1}$.

In the model (13) with the last differential equation dropped and the fraction r exogenously fixed to \bar{r} , if $k_1, k_2 > 0$ and $\frac{2\rho_1\gamma_1}{Na_1} + \frac{2\rho_2\gamma_2}{Na_2} > 1$, any $\bar{r} \in \left(1 - \frac{2\rho_2\gamma_2}{Na_2}, \frac{2\rho_1\gamma_1}{Na_1} \right)$ ensures the coexistence of both species.

In short, if there is a coexistence equilibrium for the model (13) then there is at least an \bar{r} such that also the model with r exogenously fixed converges to a coexistence equilibrium. On the contrary, if there exists an \bar{r} such that the model with r exogenous converges to a coexistence equilibrium then also the model with continuous replicator dynamics converges to a coexistence equilibrium.

4. Numerical simulations. Numerical simulations are important for shedding some light on the dynamics of the more realistic model of discrete time switching of fishing strategy. This section is mainly devoted to investigating cyclical or more complex behaviors dictated by the hybrid structure of the model, which are impossible to observe in the benchmark case of continuous switching. In fact, assuming discrete time strategy switching is more realistic than continuous time adjustments, but analytical results can be obtained under continuous adjustments (as in the previous section) and so comparisons between continuous and discrete switching are insightful. In particular, we compare here the dynamics of the system with discrete and continuous replicator equations and these cases with two simpler management strategies, namely unrestricted harvesting and splitting the fishers between the two fisheries equally. Moreover, we investigate the role played by s (the switching time) as well as the effects of nonconstant prices, i.e., demand functions (3) with slope $b_i \neq 0$, $i = 1, 2$.

Before describing and discussing the simulations, we recall that, in general, the set of fixed points of the system with a continuous time replicator is a subset of the set of fixed points of the hybrid model. Moreover, even though a fixed point under a continuous time replicator is also a fixed point in the hybrid system, its stability properties can be different, as clearly shown below.

Let us begin the numerical investigation with a complete symmetric setting of the parameter values except for the instantaneous growth rates of the two species. For illustrative purposes only, the values are chosen at the following level:

$$(20) \quad \begin{aligned} \rho_1 = 90; \quad \rho_2 = 140; \quad k_1 = k_2 = 80; \quad a_1 = a_2 = 50; \quad \gamma_1 = \gamma_2 = 9; \\ b_1 = b_2 = 0; \quad N = 40; \quad \sigma = 0.5; \quad s = 3. \end{aligned}$$

Both species are assumed to have the same carrying capacity, the same (constant) price in the market and the same cost to catch; the different intrinsic growth rates satisfy the relations $\alpha_1(1) < 0$, $\alpha_2(0) > 0$ and $k_1 > \widehat{k}_1$, so that an inner equilibrium with harvesting of both species exists and it is stable in the case of continuous time switching according to the proposition in the previous section. All the numerical simulations are obtained starting from the initial condition $X_1(0) = X_2(0) = 10$ and $r(0) = 0.5$ (which remains the same in the cases without evolutionary switching). Of course, as also shown in the first row of Figure 1, in the absence of harvesting the two noninteracting species always settle on the respective carrying capacities in the long run. Under this parameter constellation, if unrestricted oligopolistic harvesting takes place, then the first species becomes extinct (see Figure 1, row 2). On the other hand, if the exploiter is split equally in the two groups ($r = 0.5$), the trajectory converges to an equilibrium, say $E^+ = (X_1^+, X_2^+)$, with $X_2^+ > X_1^+$ (Figure 1, row 3). Instead, in the case of continuous and discrete replicator dynamics the trajectories converge to the unique (globally stable) inner equilibrium $E^* = (X_1^*, X_2^*, r^*)$ with $X_1^* = X_2^*$ and $r^* = 0.3913$ (Figure 1, rows 4 and 5).

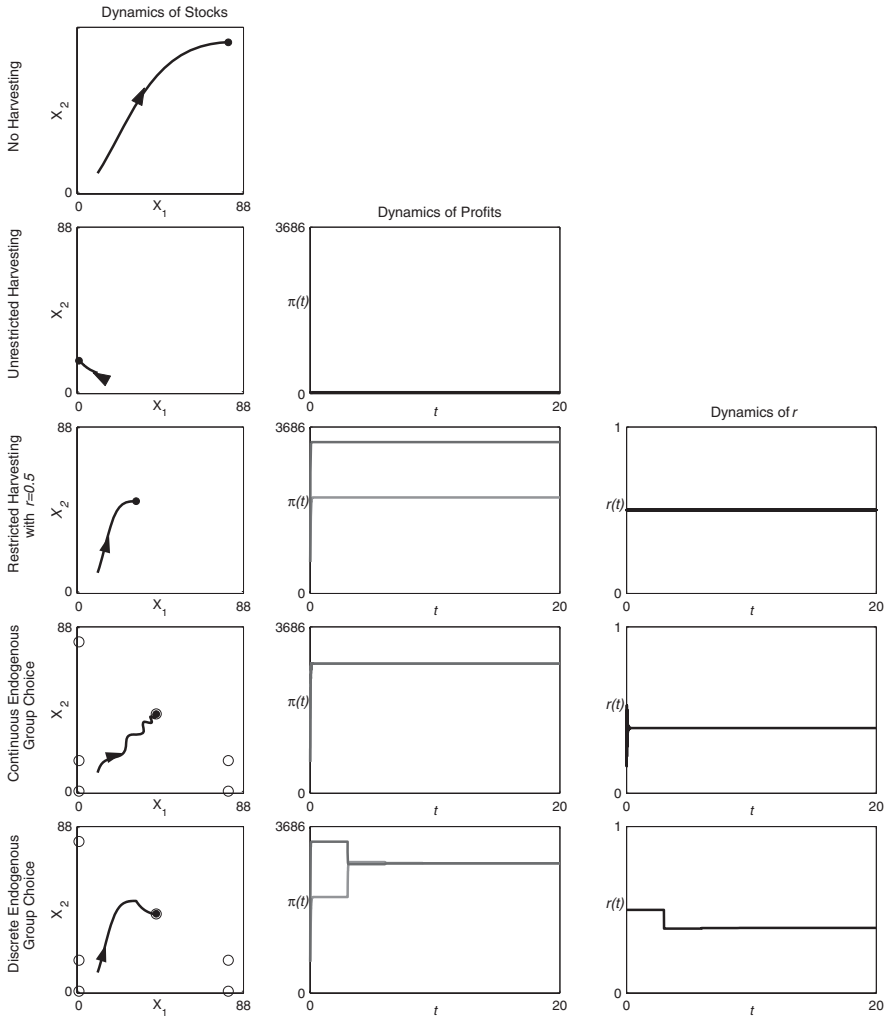


FIGURE 1. With parameters $\rho_1 = 90; \rho_2 = 140; k_1 = k_2 = 80; a_1 = a_2 = 50; \gamma_1 = \gamma_2 = 9; b_1 = b_2 = 0; N = 40; r(0) = 0.5; \sigma = 0.5; s = 3$ and initial condition $X_1(0) = 10, X_2(0) = 10$ the trajectories in the space (X_1, X_2) are represented in the first column, profits $\pi(t)$ (black line for $\pi_1(t)$ and gray line for $\pi_2(t)$) in the second column and the fraction $r(t)$ of fishers that harvest species 1 third column. Different rows represent different policies for harvesting constraints. Row 1: biological independent species with logistic growth and without harvesting. Row 2: unrestricted oligopolistic harvesting. Row 3: two groups of fishers each harvesting only one species with imposed fraction $r = 0.5$. Row 4: endogenously adjusting $r(t)$ according to a continuous time replicator dynamics. Row 5: hybrid model with $r(t)$ evolving according to discrete time replicator dynamics.

In the case of continuous time replicator dynamics, this confirms the analytical results of the previous section. Moreover, the numerical simulation shows that the same asymptotic dynamics occur in the case of impulsive adjustment in discrete time as well, even if a difference can be seen in the initial transient part of the trajectory. Since by assumption it is $\alpha_1(1) < 0$, it is not sustainable to let all agents harvest species 1, so that $E_2^2 = (k_1(1 - N \frac{a_1}{2\gamma_1\rho_1}), k_2, 1)$ is not a feasible equilibrium of the model under replicator dynamics. On the other hand, all the other border equilibria described in the proposition “boundary equilibria and their stability” exist and are unstable, as shown in Figure 1. This means that under replicator dynamics the system is able to adjust endogenously the two fractions of fishers that harvest species one or two, putting less fishing pressure on the species with lower growth rate (species one in this specific example). This avoids the overexploitation of the species with respect to the other. In other words, this is a clear example of an autonomous self-regulating system. Moreover, even from an economic point of view, in this case the evolutionary mechanism represents a good solution ensuring a higher level of average profits, as shown in the second column of Figure 1 depicting the corresponding profits versus time. As well, the distribution of profits between fishers in the two groups also appears fairer in the case of evolutionary strategy switching (in both continuous and discrete time) than in the other cases.

It is interesting to observe, from the analytical expression of the inner equilibrium X_i^* in (17), that only asymmetries in the values of the economic parameters a_i and γ_i , $i = 1, 2$, can create differences in the long-run levels of biomass of the two species. For this reason, Figure 2 is obtained under the same parameters of Figure 1 but with a decreased value of the cost parameter $\gamma_1 = 5$, i.e., catching fish 1 becomes less expensive. The trajectory of the dynamical system with continuous replicator converges to the inner equilibrium $E^* = (X_1^*, X_2^*, r^*)$ for which $X_1^* < X_2^*$, while the trajectory of the dynamical system with a discrete replicator converges to a closed invariant orbit surrounding the equilibrium E^* , suggesting its instability under discrete switching, see the last row of Figure 2. Here the dynamics are cyclic around the unstable fixed point, and this is due to the hybrid nature of the dynamical system with discrete replicator equations and can not be observed in the other dynamical models here considered.

Concerning the profits for the different harvesting strategies, the system with (continuous or discrete) replicator dynamics is able to ensure higher income for operators than in the other cases. In fact, with unrestricted oligopolistic harvesting, the extinction of one species and the depletion of the other occur due to overfishing, which sharply reduces total average profits, see again Figure 2, second column. Note that fixing the fraction of exploiters (recall that here we assumed $r = 0.5$) can even lead to higher profits, but at the cost of the extinction of the first species, so that half of the fishers (the ones who are exogenously assigned to harvest species one only) are forced to abandon their activity because there is no longer stock

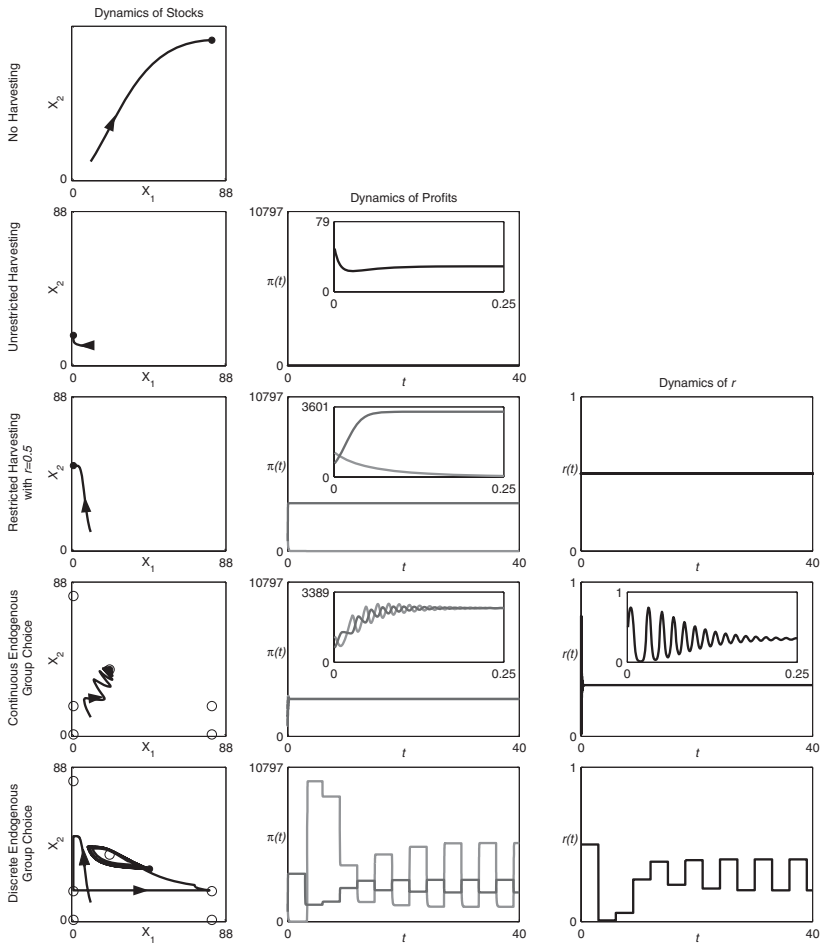


FIGURE 2. Initial condition and parameters as in Figure 1, except parameter $\gamma_1 = 5$. The explanation of the panels is the same as in Figure 1.

to harvest for them (see Figure 2, row 3). It follows that, despite the high level of total profits generated with the fixed fraction, this is not a desirable situation indeed.

For the sake of comparison between the cases in Figures 1 and 2, it is interesting to investigate the reasons why the extinction of species 1 occurs only in the case of Figure 2, when r is exogenously determined. From the analytical results, every time the evolutionary mechanism settles endogenously to the level r^* ensuring the coexistence of the two species, it is possible to fix exogenously an \bar{r} that ensures the coexistence and vice versa. However, to fix exogenously an \bar{r} requires correctly

estimating the parameters of the model and their possible changes over time and to adjust r accordingly and immediately in case of relevant changes in these values. On the contrary, the evolutionary mechanism is able to react endogenously to changes in the economical and biological parameters without requiring any external intervention, thus ensuring the coexistence of the two species (whenever the conditions stated in the previous section hold). This represents an important advantage of the evolutionary model that justifies its use. This aspect can be better appreciated by a cross simulation analysis. Starting from the simulation represented in Figure 1, fixing exogenously $r = 0.5$ is enough to ensure the coexistence of the two species, as condition $\frac{2\gamma_1\rho_1}{a_1N} = 0.81 \in (0.5, 1.81)$ is fulfilled, see 18. However, if the cost parameter γ_1 decreases from 9 to 5 as in Figure 2 (e.g., because a new fishing technique has been introduced), then it is $\frac{2\gamma_1\rho_1}{a_1N} = 0.45 \in (0, 0.5)$ so that species 1 goes extinct, see (19). Therefore, in the case of a fixed r , if this value is not reduced exogenously by the authority, the risk of extinction of one of the two shellfish species is high, as happens in Figure 2 second row. In this specific case, the fixed value of r should be in the range $(0, 0.45)$ in order to avoid the extinction of species 1. As it is clear from this example, this requires continuous monitoring of the system (biological and economical parameters). On the contrary, the evolutionary mechanism is able to adjust r autonomously avoiding the risk of extinction of species.

Another key aspect that deserves to be deepened is the different dynamics of the models with continuous and discrete replicator dynamics, i.e., the effects of s on the dynamics of the model. It is worth noticing that s , the time interval after which the fishers can choose to change their fishing strategy, influences the amplitude of the oscillations. When $s \rightarrow 0$ the amplitude tends to zero, and the hybrid dynamical system has a behavior similar to the one obtained with a continuous replicator dynamic. However, when s increases, the presence of cycles of greater amplitude can be detected, see Figure 3. From the two pictures in Figure 3, it is easy to see that the orbits surrounding the inner equilibrium are characterized by two switching times, i.e., they are of period $2s$. Along these orbits the biomass levels of the two species always move in opposite directions, one increases and one decreases, this opposite relationship of growth changes at each switching time according to $r(t)$, which takes two values $\{\underline{r}_s, \bar{r}_s\}$ along the orbits depending on s .

Let us now consider the same values for parameters as in Figures 2 and 3 changing the level of the carrying capacity of species 2 only, namely $k_2 = 10$. For the dynamical system with continuous replicator dynamics, the inner equilibrium $E^* = (X_1^*, X_2^*, r^*)$ is positive, hence it is stable according to Proposition 2 in the previous section. More precisely, this is the situation described in case 3 of Proposition 2. Regarding the system with discrete replicator equations, Figure 4 shows some dynamical behaviors of the hybrid model for different values of the switching time s . Numerical evidence shows that the inner equilibrium is unstable under the adaptive discrete dynamics. For $s = 1$ the trajectory passes very close to the inner equilibrium and draws a quite erratic path around it. For $s = 3$ and 10 more regular

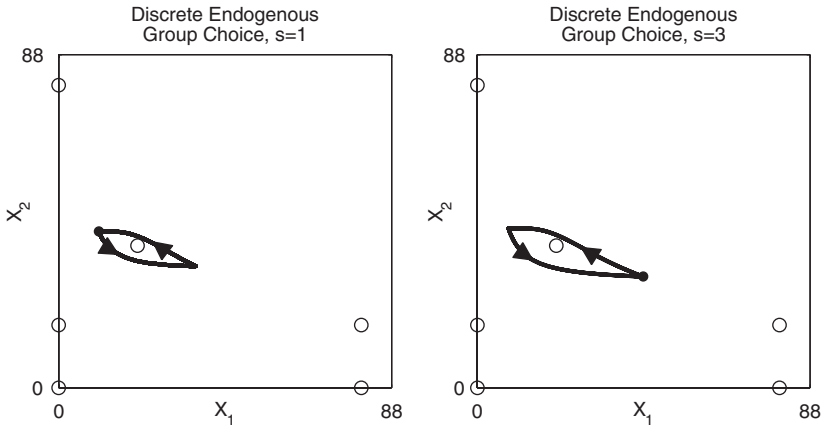


FIGURE 3. Two trajectories in the space (X_1, X_2) with initial condition and parameters as in Figure 2 for the dynamical model with discrete replicator equation. The picture gives evidence of how the amplitude of the closed orbits changes by changing the switching time interval s , with $s = 1$ in the left panel and $s = 3$ in the right panel.

orbits can be observed. The time series of the individual and total profits are quite irregular as well, see the last column of Figure 4. It is worth noticing that profits arising from fishing species 1 (black lines) are quite regular along their time series. Instead, the profits arising from fishing species 2 (gray lines) exhibit a quite irregular pattern with long periods characterized by high profits and short periods characterized by low profits.

Numerical simulations are also useful for obtaining some insights on how decreasing inverse demand functions can influence the dynamic behaviors of the models studied here. If we repeat all the numerical simulations performed in the previous examples with $b_i \neq 0$, $i = 1, 2$, we see that the total harvesting and profits decrease, but in general the positive effects of the switching mechanism on reducing overexploitation of the two fish species can still be appreciated. In order to give an idea of the difference between the dynamics of the models with negative slopes of the inverse demand functions (3), i.e., decreased prices with increased total harvesting, Figure 5 shows the dynamics of the models with $b_i = 0.05$, $i = 1, 2$ and the other parameters values as in Figure 1. As for the case with zero slope demand, the model with unrestricted harvesting leads to the extinction of species 1. On the other hand, when r is defined exogenously or endogenously by fishers under a profit-driven adaptive process, it is possible to prevent species one from extinction and increase the general level of profits (see Figure 5).

The positive effect of the switching mechanism can be appreciated even for larger values of b_i , $i = 1, 2$. In order to avoid too much harvesting reduction due to demand effects, in Figure 6 we modify the parameter values as follows:

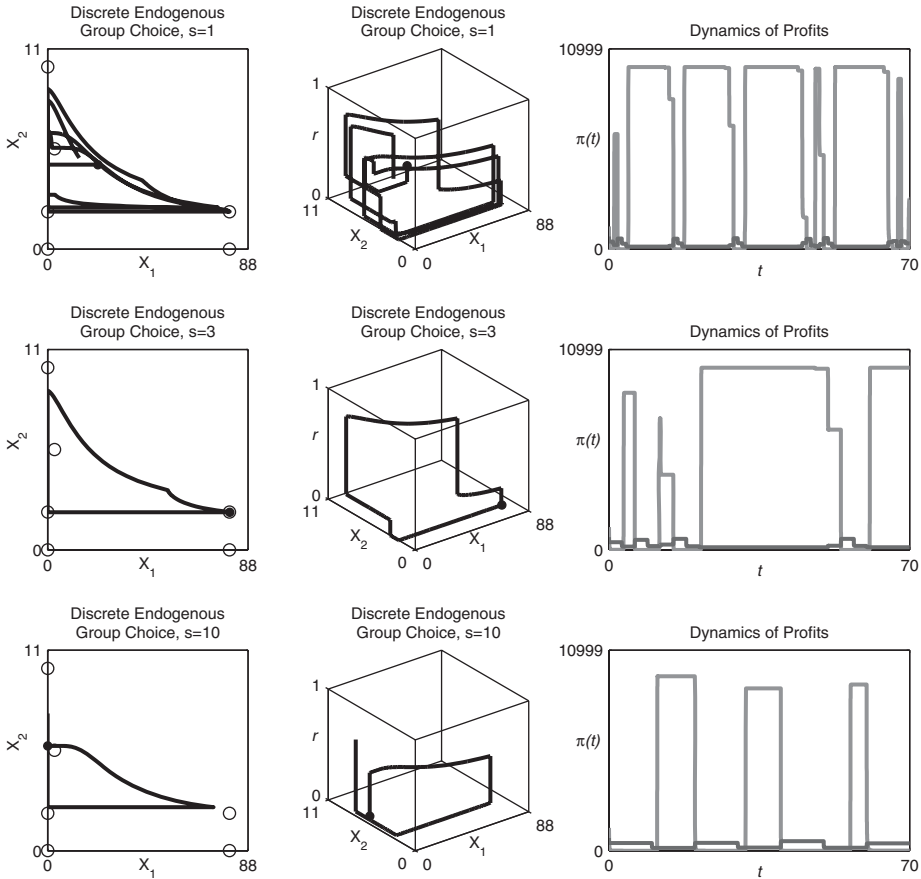


FIGURE 4. For the hybrid dynamic model with initial condition and parameters as in Figure 2 but $k_2 = 10$. In the first column the trajectories are projected in the space (X_1, X_2) ; in the second column the same trajectories are represented in the phase space (X_1, X_2, r) and in the third column the versus-time representation of profits along the trajectories are represented for both fishers harvesting species 1 (black line) and 2 (gray line), respectively. The different rows are obtained for different values of the discrete switching time s , given by $s = 1, 3$, and 10 , respectively.

$$\rho_1 = 80; \rho_2 = 140; k_1 = 50; k_2 = 80; a_1 = 220; a_2 = 200; \gamma_1 = \gamma_2 = 9;$$

$$b_1 = b_2 = 0.1; N = 40; \sigma = 0.5; s = 3.$$

With respect to the other examples, the reservation prices have been increased and the growth rate and the carrying capacity for species one have been decreased. Having a smaller carrying capacity, species 1 is more rare in nature than species 2 and thus has a higher reservation price. The numerical simulations in Figure 5

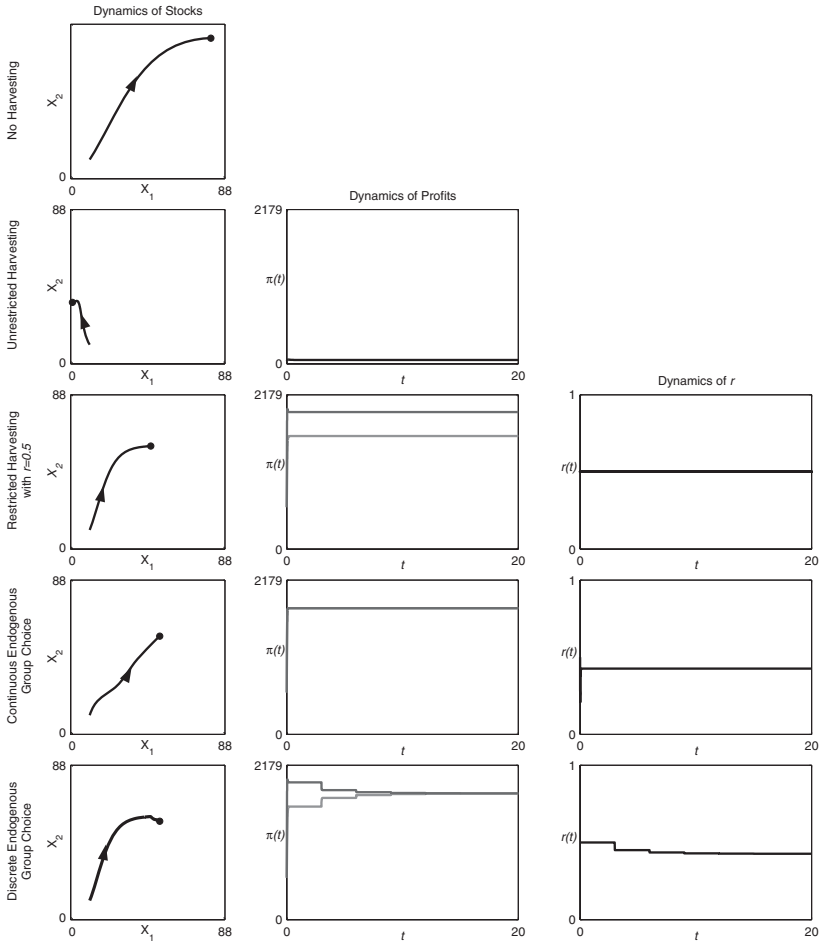


FIGURE 5. Same parameter values and initial conditions as in Figure 1 but $b_1 = b_2 = 0.05$. The meaning of the panels is the same as in Figures 1 and 2.

gives evidence of overexploitation in the cases of unrestricted harvesting and restricted harvesting with a fixed proportion of exploiters. In both cases, the level of harvesting is not sustainable over time and in the long run the species with the lower intrinsic growth rate will go extinct. However, when fishers can adjust their strategy myopically according to past profits, the extinction problem for species with lower growth rate could be avoided. It is worth noticing that, with these parameter values, the discrete switching mechanism performs even better than the instantaneous one. In fact, the first mechanism ensures a level of profits at least as high as the second one and the biological equilibrium has higher level of biomass

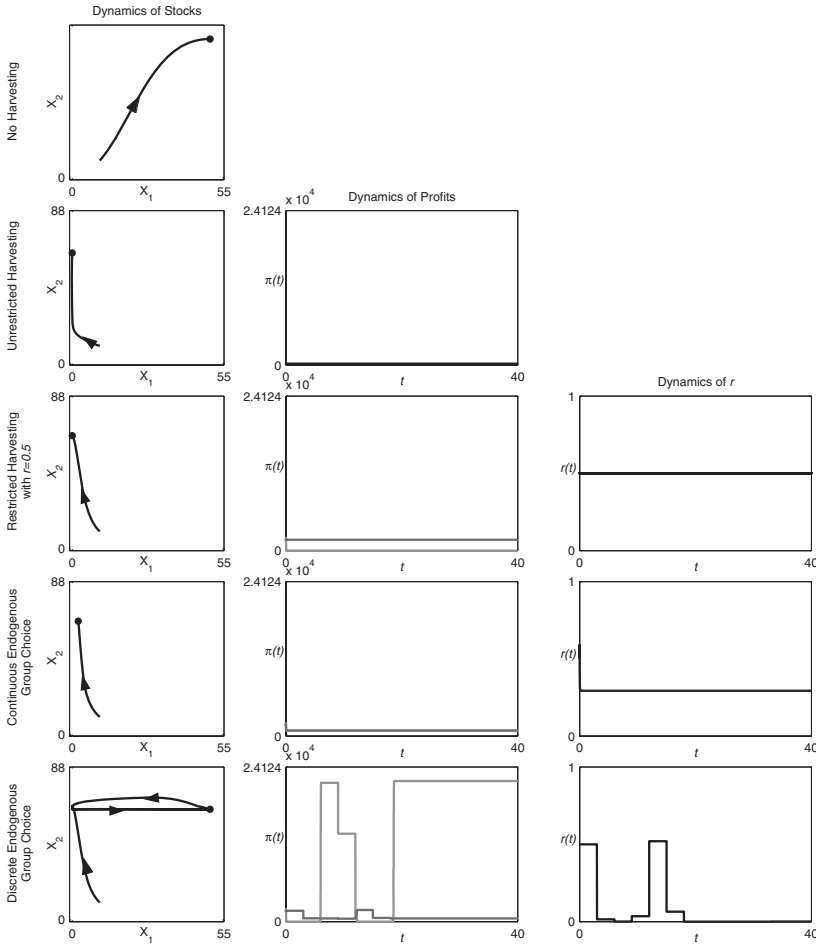


FIGURE 6. Same initial conditions as in Figure 2 and parameters $\rho_1 = 80; \rho_2 = 140; k_1 = 50; k_2 = 80; a_1 = 220; a_2 = 200; \gamma_1 = \gamma_2 = 9; b_1 = b_2 = 0.1; N = 40; r(0) = 0.5; \sigma = 0.5; s = 3$. The meaning of the panels is the same as in Figures 1 and 2.

for both species, so that there is a higher probability of surviving in the long run even in presence of exogenous shocks, which may temporarily reduce the natural rate of growth of the two (shell)fish species.

5. Conclusions. This paper proposes a dynamical system to model a fishery where two noninteracting fish species are harvested by a population of fishers, each allowed to catch just one species at a time and with the possibility of changing their fishing choice at specific times, according to a profit-driven replicator dynamic. The

dynamic model is hybrid, since the growth of fish species as well as harvesting activities occur in continuous time, whereas decisions about the species to catch take place in discrete time.

The analytical and numerical results show that this type of evolutionary mechanism may lead to a good compromise between total profit maximization, profit distribution among fishers and resource conservation, thanks to evolutionary self-regulation mainly based on cost externalities. In fact, the reduction of biomass of one species leads to its increasing landing cost and, consequently, favors the endogenous switching to the more abundant species. Moreover, severe overfishing of one species causes decreasing prices and consequently decreasing profits. Of course, in cases where both fisheries are declining in terms of both stocks and profits, the evolutionary switching method proposed can at most allow fishers to move to the least-bad fishery, with the only result of slackening fishery decline.

Some simpler benchmark cases, with fixed prices and/or continuous time switching, have also been developed here. These benchmarks constitute a useful guide, even a sort of basic foundation, on which the (mainly numerical) analysis of the more realistic model can be performed, namely with variable market prices and discrete strategy switching.

The model studied in this paper offers a glimpse into the interesting properties of myopic and adaptive harvesting mechanisms driven by endogenous evolutionary processes. However, this is just a starting point for further and deeper analysis. There are several aspects of the model that deserve to be explored more deeply. For example, the variable r , i.e., the fraction of fishers harvesting a given fish stock, is assumed to unconstrainedly range in the interval $[0, 1]$, where 0 and 1 are always equilibria. Indeed, when r converges to 0 or 1, one of the two species is no longer harvested and consequently it is not available in the market. This could be a reasonable practice only if the two species are perfect substitutes in consumer tastes (corresponding to the case $\sigma = 1$ in our model). Otherwise consumers may be heavily penalized by such an outcome. This issue will be addressed in future work, for example by introducing constraints on the dynamics of r or by assuming that the fractions of fishers harvesting one of the two species have a fixed component and a time varying portion, so that the nonswitching portion ensures that both fish species are always available in the market. The endogenously switching components, on the other hand, help to regulate the fishing pressure so that the more abundant species is more harvested due to lower costs. The research can be extended in other different directions as well, for example it would be interesting to compare the results obtained here for the endogenous and myopic adaptive switching process with those obtained in models where an optimal fraction r is computed according to an optimal control problem, in which a regulator maximizes a social welfare function over a planning horizon. Another interesting extension is to formulate the problem in terms of choosing effort and then include a constraint on total effort in the fishers' profit maximization problems of restricted and unrestricted harvesting.⁴ The same

arguments may be applied to the choice of an optimal length s of the switching interval, since it seems to be an important parameter in our numerical experiments. Moreover, the stability analysis for the model with continuous evolutionary switching mechanisms may be extended by using more sophisticated mathematical tools to provide qualitative indications on the behavior of the hybrid dynamical in the long run. Finally, the model can also be extended to the case of interacting species. For example, a similar model has been proposed by the same authors in Bischi et al. [2012] for the simulation of a fishery where a predator–prey system is exploited in the presence of the same endogenous evolutionary self-regulating method. Even if it is quite difficult to harvest only a single species when two fish populations interact in the same environment, the simulation of such a situation can provide useful theoretical information on the understanding of the trade-off between species interactions and endogenous evolutionary processes based on economic forces.

ENDNOTES

1. In the context we are considering, we disregard the case $\sigma < 0$, related to varieties that are demand complementary.
2. Specific conditions can be given for the sufficiency of these conditions, i.e., for the concavity of profit π_q^F with respect to $h_{1,q}^F$ and $h_{2,q}^F$. For instance, in the case $b_1 = b_2$ (assumption that will be considered in the following) it is easy to prove that profits are strictly concave. However, we can assume by continuity that the same holds for $b_1 \simeq b_2$.
3. Notice that in the hybrid system (11) the time index t has to be explicitated in order to ensure synchronism between discrete and continuous dynamical variables.
4. We thank an anonymous referee for suggesting this enhancement of the basic model.

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APPENDIX

Cost function. Following Szidarovszki and Okuguchi [1998], Clark [1990], and Conrad and Smith [2012], we obtain here the cost function (4) employed in the profit maximization problems. Let us assume that current harvesting h is obtained through a Cobb–Douglas production function of the stock X and fishing effort E

(see e.g., Clark [1990], pp. 222–223.) with total factor productivity ρ

$$h(X, E) = \rho X^\alpha E^\beta$$

from which $E = \rho^{-1/\beta} X^{-\alpha/\beta} h^{1/\beta}$. Moreover, assuming that the “production function” $h(X, E)$ is an homogeneous function of degree 1 with $\alpha = \beta = \frac{1}{2}$ and that total cost of fishing is proportional to exerted effort, i.e., $C = \delta E$, then it is

$$C = \delta \rho^{-2} X^{-1} h^2 = \gamma \frac{h^2}{X}.$$

Without loss of generality, we assume that $\rho = 1$, so that γ can be interpreted as a cost parameter.

Proof of Proposition 1. Any steady state of the dynamical system (13) must satisfy the algebraic system:

$$\begin{cases} X_1 \left(\rho_1 \left(1 - \frac{X_1}{k_1} \right) - Nr \frac{a_1}{2\gamma_1} \right) = 0 \\ X_2 \left(\rho_2 \left(1 - \frac{X_2}{k_2} \right) - N(1-r) \frac{a_2}{2\gamma_2} \right) = 0 \\ r(1-r) \left[\frac{a_1^2 X_1}{4\gamma_1} - \frac{a_2^2 X_2}{4\gamma_2} \right] = 0 \end{cases}$$

from which we get the equilibria E_j^k , $k = 0, 1, 2$ and $j = r, 1, 2$ listed in the Proposition 1. The Jacobian matrix for the dynamical system (13) is given by

$$J(X_1, X_2, r) = \begin{bmatrix} \alpha_1(r) - \frac{2\rho_1 X_1}{k_1} & 0 & -N \frac{a_1 X_1}{2\gamma_1} \\ 0 & \alpha_2(r) - \frac{2\rho_2 X_2}{k_2} & N \frac{a_2 X_2}{2\gamma_2} \\ r(1-r) \frac{a_1^2}{4\gamma_1} & -r(1-r) \frac{a_2^2}{4\gamma_2} & (1-2r) \left[\frac{a_1^2 X_1}{4\gamma_1} - \frac{a_2^2 X_2}{4\gamma_2} \right] \end{bmatrix}.$$

Evaluated at the equilibria with extinction of both species $E^0 = (0, 0, r)$, the Jacobian is the following triangular matrix:

$$J(E^0) = \begin{bmatrix} \alpha_1(r) & 0 & 0 \\ 0 & \alpha_2(r) & 0 \\ r(1-r) \frac{a_1^2}{4\gamma_1} & -r(1-r) \frac{a_2^2}{4\gamma_2} & 0 \end{bmatrix}$$

from which it follows that the eigenvalues are the entries in the main diagonal, so we get the statement for the nonhyperbolic stability given in the proposition.

Without loss of generality, in the rest of the proof we assume that only the second species is harvested ($r = 0$), as with $r = 1$ one has just to swap indexes in the first two coordinates of the equilibria and the stability analysis is the same. Let us consider the equilibrium where species 1 is at the carrying capacity and species 2 vanishes, i.e., $E_1^0 = (k_1, 0, 0)$

$$J(E_1^0) = \begin{bmatrix} -\rho_1 & 0 & -N \frac{a_1 k_1}{2\gamma_1} \\ 0 & \alpha_2(0) & 0 \\ 0 & 0 & \frac{a_1^2 k_1}{4\gamma_1} \end{bmatrix}.$$

The Jacobian matrix assumes again a triangular structure, with eigenvalues $-\rho_1 < 0$ and $\frac{a_1^2 k_1}{4\gamma_1} > 0$ so E_1^0 is always a saddle point. At the fixed point $E_1^1 = (0, k_2(1 - N \frac{a_2}{2\gamma_2 \rho_2}), 0)$ the Jacobian matrix becomes

$$J(E_1^1) = \begin{bmatrix} \rho_1 & 0 & 0 \\ 0 & -\alpha_2(0) & N \frac{a_2 k_2}{2\gamma_2 \rho_2} \alpha_2(0) \\ 0 & 0 & -\frac{a_2^2 k_2^2}{4\gamma_2 \rho_2} \alpha_2(0) \end{bmatrix}$$

whose eigenvalues are $\rho_1 > 0$, whereas the other two are negative provided that $\alpha_2(0) > 0$, i.e., $Na_2 < 2\gamma_2 \rho_2$, whereas if the reverse inequality holds the second component of the equilibrium becomes negative. Finally, at $E_1^2 = (k_1, k_2(1 - N \frac{a_2}{2\gamma_2 \rho_2}), 0)$ we have

$$J(E_1^2) = \begin{bmatrix} -\rho_1 & 0 & -N \frac{a_1 k_1}{2\gamma_1} \\ 0 & -\alpha_2(0) & \frac{a_2 N k_2}{2\gamma_2 \rho_2} \alpha_2(0) \\ 0 & 0 & \frac{a_1^2 k_1}{4\gamma_1} - \frac{a_2^2 k_2}{4\gamma_2 \rho_2} \alpha_2(0) \end{bmatrix}.$$

By the previous discussion, the first two eigenvalues are negative provided that $\alpha_2(0) > 0$, i.e., $Na_2 < 2\gamma_2 \rho_2$. In this case the third eigenvalue is also negative whenever $\alpha_2(0) > \rho_2 \frac{a_1^2 k_1 \gamma_2}{a_2^2 k_2 \gamma_1} (> 0)$, which is equivalent to condition (15).

Proof of Proposition 2. From the definition of equilibrium we have that $X_i^* = k_i \left(1 - Nr_i^* \frac{a_i}{2\gamma_i \rho_i}\right) = \frac{k_i}{\rho_i} \alpha_i(r_i^*)$, where $r_1^* = r^*$ and $r_2^* = 1 - r^*$, i.e., $X_i^* > 0 \Leftrightarrow \alpha_i(r_i^*) > 0$. By solving inequalities $\alpha_i(r_i^*) > 0$, $i = 1, 2$ with the condition $1 > r^* > 0$, we get the different cases described in the proposition. Concerning the stability, the Jacobian matrix evaluated at the inner equilibrium $E^* = (X_1^*, X_2^*, r^*)$ can be rewritten as

$$J(E^*) = \begin{bmatrix} -\alpha_1(r^*) & 0 & -N \frac{a_1 X_1^*}{2\gamma_1} \\ 0 & -\alpha_2(r^*) & N \frac{a_2 X_2^*}{2\gamma_2} \\ r^*(1-r^*) \frac{a_1^2}{4\gamma_1} & -r^*(1-r^*) \frac{a_2^2}{4\gamma_2} & 0 \end{bmatrix}.$$

Thus, at the equilibrium the Jacobian matrix has the structure

$$J(E^*) = \begin{bmatrix} J_{11} & 0 & J_{13} \\ 0 & J_{22} & J_{23} \\ J_{31} & J_{32} & 0 \end{bmatrix},$$

where the elements J_{11} , J_{22} , J_{13} , and J_{32} are negative and J_{23} and J_{31} are positive. Therefore, for the characteristic polynomial

$$\lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3$$

with

$$\begin{aligned} a_1 &= J_{11} + J_{22}; & a_2 &= -J_{23}J_{32} - J_{31}J_{13} + J_{11}J_{22}; \\ a_3 &= J_{13}J_{22}J_{31} + J_{11}J_{23}J_{32} \end{aligned}$$

satisfies the Routh–Hurwitz criterion, as

$$a_1 > 0; \quad a_2 > 0; \quad a_3 > 0$$

and

$$a_1 a_2 - a_3 = -J_{11} J_{22} (J_{11} + J_{22}) + J_{11} J_{13} J_{31} + J_{23} J_{32} (2J_{11} + J_{22}) > 0.$$

Therefore, whenever the equilibrium $E^* = (X_1^*, X_2^*, r^*)$ is feasible (i.e., it involves positive biomasses), it is also stable.

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