Research paper

# Stability, bifurcations and hydra effects in a stage-structured population model with threshold harvesting

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## ARTICLE INFO

## ABSTRACT

In this paper, we investigate the dynamics of a discrete-time stage-structured population model where juveniles and adults may be subject to threshold harvesting. This management policy allows the harvesting of the target population only if its size exceeds a predetermined threshold. It is commonly used for maintaining biomass, obtaining a higher yield, and preventing population collapse. We focus on the response of the structured populations to harvesting and study how they can be affected by considering different thresholds for each age class. We find all possible equilibria of the system and analyze their stability; we show that harvesting does not destabilize globally stable equilibria. We discuss when hydra effects may occur, more specifically, we determine when the adult population size can increase at equilibrium in response to an increase in its per-capita mortality rate as a consequence of threshold harvesting. A rigorous 2-parameter bifurcation diagram is given for semelparous populations, which helps to understand the general case when adult survivorship rates are low. Numerical results complement the bifurcation analysis in the general case.

## 1. Introduction

This work is concerned with the study of biologically motivated discrete-time model arising in ecology when populations are subject to human management, aimed at exploitation (e.g., hunting, fishing), conservation of endangered species, or control of nuisance species. These models are popular objects of research in population management and they provide insight into the mechanisms of conservation of threatened species and eradication of invasive species. The common thread is a predetermined threshold which guarantees either that exploitation rates at low stock sizes is reduced or completely eliminated, or that pest control is activated when an environmental or economic injury level is exceeded. These considerations lead to the study of threshold harvesting rules [1,2]. Roughly speaking, these rules establish a threshold biomass below which no harvest/control is permitted. As pointed out in [3], *"thresholds are a necessary feature of any harvesting strategy with the objective of minimizing risks of resource depletion or extinction while optimizing yields in variable environments"*.

Recently, different forms of threshold harvesting (TH, for short) have been studied in the framework of one-dimensional discrete models [4–8], revealing a rich dynamics due to both smooth and border-collision bifurcations typical of piecewise-smooth maps [9,10]. In this paper, by TH we understand that the total population (or the population of a particular stage)

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above a given threshold is removed every year; see [6, Table 1] for a collection of other names and contexts where threshold harvesting has appeared in the literature. In particular, a typical name is *fixed escapement*, and this fishery policy is frequently used in Pacific salmon management [11, p. 440]. See [1,2] for more examples of fisheries jurisdictions that have adopted some form of threshold harvest control rule. The utility of fixed escapement harvesting policies has been also supported by experimental results (see, e.g., [12]).

Knowing the response (both qualitative and quantitative) of populations to harvesting is crucial, and an important question is the way in which harvesting affects population abundance and stability, which could be sometimes counterintuitive.

In the absence of harvesting, the dynamics of a single-species population without migration whose changes are due to birth and death can be described by the first-order difference equation

$$x_{n+1} = f(x_n), \tag{1.1}$$

for an initial value $x_0 > 0$, where the map $f$ is the stock-recruitment function [11]. If, instead, the population is managed by a TH policy, then the population dynamics is governed by the recurrence

$$x_{n+1} = \psi(x_n) := \min\{f(x_n), T\} = \begin{cases} f(x_n) & \text{if } f(x_n) \le T; \\ T & \text{if } f(x_n) > T; \end{cases} \tag{1.2}$$

where $T > 0$ is the threshold. Eq. (1.2) assumes that harvesting occurs after reproduction, or, more properly, population stock at the generation $n + 1$ is measured after harvesting (see [13] for further discussions on the order of events in discrete-time population models with only two processes: reproduction and harvesting). TH models are typically managed by a flat-topped map $\psi$; we refer to [14,15] and the discussion in [6] for some dynamical aspects of recurrences in this framework.

As far as we know, an analytical study of threshold rules has not been addressed in the context of discrete-time stage-structured models, although some numerical results can be found in [16]. Studying how harvesting influences the dynamics of structured populations is especially important because empirical evidence suggests that stage-specific forms of control or harvesting can lead to unexpected outcomes [17–19]. One of these outcomes is known as the hydra effect, which is when a population increases in response to an increase in its per-capita mortality rate [20] (see also [18] and its references, for recent discussions). In threshold harvesting models, it is interesting to look for hydra effects when the threshold becomes smaller since it results in an increase of harvest intensity (and hence in mortality). In a structured population model involving juveniles and adults, the possibility of hydra effects in adult population was rigorously studied in [21] when proportional harvesting (PH, for short) is used. PH means that a fixed percentage of the juvenile or the adult population, or both, is harvested every year. In this work, by implementing a TH strategy instead of a PH one, we find necessary and sufficient conditions for hydra effects for the same stage-structured model.

Another possible effect of harvesting rules is the destabilization of a stable equilibrium which leads to population cycling or chaos. For recent related results concerning one-dimensional maps, we refer to [22] (and references therein). We also recall that TH in one-dimensional maps has a stabilizing effect, namely a globally stable equilibrium cannot be destabilized when harvest intensity is increased by decreasing the threshold (see [6]). Using an enveloping technique for difference equations due to El-Morshedy and Jiménez López [23], we prove in Section 3 that the robust stability properties of TH remain valid for the considered family of stage-structured population models. This is in contrast with the results obtained in [19,21] concerning stage-structured populations subject to PH. In fact, increasing harvest intensity by decreasing any of the thresholds (in juvenile or adult populations) cannot destabilize a stable population in our model.

At last, it is worth noticing that TH can induce unusual bifurcations, like the so-called border-collision bifurcations (BCB, for short). This phenomenon has been observed for one-dimensional maps resulting from different harvest control rules [8]. We notice that, when two age classes are considered, the harvesting model is represented by a second-order difference equation (see (2.3)), which makes the bifurcation study more complicated than in the first-order case. We perform a bifurcation analysis for a case study of semelparous populations (i.e., when adults do not survive the reproductive season) showing the occurrence of BCBs for a related first-order difference equation, and then we use it for the second-order equation. Finally, we give some insight into the role of adult survivorship rates, which are generally stabilizing, as noticed in related models [24,25].

The paper is organized as follows. In Section 2, we describe the stage-structured model subject to a TH strategy. In Section 3, we discuss the existence of equilibria and their stability. In Section 4, we investigate hydra effect phenomena. In Section 5, we explore the global dynamics of the semelparous and iteroparous population through a bifurcation analysis which includes both 1-parameter and 2-parameter bifurcation diagrams. In Section 6, we conclude our study with a discussion.

## 2. Stage-structured model with threshold harvesting

In this section, we introduce the stage-structured model managed by threshold harvesting we are dealing with. The interested reader can find different models and many applications for structured populations in [26].

Looking at populations with two age classes, let $A_n$ and $J_n$ be respectively the population size of adults and juveniles at generation $n = 0, 1, \dots$ The survivorship rate of the adult class is denoted by $s_a$ and the one of the juvenile by $s_j$, with $s_j \in (0, 1]$ and $s_a \in [0, 1)$.

As a stock-recruitment function, we consider a map $f$ such that:

(H1) $f : [0, +\infty) \to [0, +\infty)$ is continuous, has a unique positive fixed point $f(1) = 1$, $f(x) > x$ for every $x \in (0, 1)$, and $0 < f(x) < x$ for every $x \in (1, +\infty)$.

Notice that conditions in (H1) are typical of population models without Allee effect where, without loss of generality, one can consider a normalized model with positive equilibrium at $x = 1$. For a list of stock-recruitment functions used in fisheries and satisfying (H1) (corresponding to compensatory and overcompensatory population models), see [11, Chapter 3]. A prototypical example is given by the scaled exponential Ricker-type nonlinearity

$$f(x) = xe^{r(1-x)}, \tag{2.1}$$

where $r > 0$ is the growth rate parameter (see [27]).

We denote the population sizes of juveniles and adults after harvesting by $h_j(J)$ and $h_a(A)$, respectively. Following [19,21], the model is defined by the following system:

$$\begin{cases} A_{n+1} = s_a h_a(A_n) + s_j h_j(J_n), \\ J_{n+1} = f(h_a(A_n)). \end{cases} \tag{2.2}$$

Notice that the planar system (2.2) can be equivalently written as the second-order difference equation

$$A_{n+1} = s_a h_a(A_n) + s_j h_j(f(h_a(A_{n-1}))), \tag{2.3}$$

with initial conditions $A_0 > 0$, $A_1 > 0$.

In this paper we assume $s_j = 1 - s_a$, which is one of the scenarios considered by Zipkin et al. [19] and Liz and Pilarczyk [21]. It encapsulates situations in which juvenile and adult survivals trade off such that one is low when the other is high, or when both are equally intermediate. Other scenarios are of course possible, but are not the subject of this work.

Thus, throughout our analysis, we restrict to consider the survivorship rate of adults $s_a = \alpha$ and the corresponding survivorship rate of juveniles $s_j = 1 - \alpha$. Results are thus given for the equation

$$A_{n+1} = \alpha\, h_a(A_n) + (1 - \alpha) h_j\left(f(h_a(A_{n-1}))\right), \tag{2.4}$$

depending on the real parameter $\alpha \in [0, 1)$.

Assuming that populations of juveniles and adults are managed by threshold harvesting, and denoting by $T_j$ and $T_a$ the thresholds for juveniles and adults, respectively, we consider three possibilities:

(JH) Juvenile-only harvest ($h_a(x) = x$, $h_j(x) = \min\{x, T_j\}$):

$$A_{n+1} = \alpha A_n + (1 - \alpha) \min\{f(A_{n-1}), T_j\}. \tag{2.5}$$

(AH) Adult-only harvest ($h_j(x) = x$, $h_a(x) = \min\{x, T_a\}$):

$$A_{n+1} = \alpha \min\{A_n, T_a\} + (1 - \alpha)f\left(\min\{A_{n-1}, T_a\}\right). \tag{2.6}$$

(BH) Both age classes are harvested ($h_j(x) = \min\{x, T_j\}$, $h_a(x) = \min\{x, T_a\}$):

$$A_{n+1} = \alpha \min\{A_n, T_a\} + (1 - \alpha) \min\left\{T_j, f\left(\min\{A_{n-1}, T_a\}\right)\right\}. \tag{2.7}$$

We use the acronyms (JH), (AH) and (BH) in the paper to make clear which strategy is being considered.

## 3. Equilibria and stability results

The following results concern the equilibria of the general case (BH), and in particular those of (JH) and (AH).

**Proposition 3.1.** *Assume* (H1). *Then model (BH) given by* (2.7) *has a unique positive equilibrium $p$, which is:*

*(i)   $p = 1$, if $1 \leq \min\{T_a, T_j\}$;*
*(ii)  $p = T_j$, if $T_j \leq \min\{T_a, 1\}$;*
*(iii) $p = \alpha T_a + (1 - \alpha) \min\{T_j, f(T_a)\}$, if $T_a \leq \min\{T_j, 1\}$.*

**Proof.** It is clear that $p$ is an equilibrium of (2.7) if and only if

$$p = \alpha \min\{p, T_a\} + (1 - \alpha) \min\left\{T_j, f\left(\min\{p, T_a\}\right)\right\}. \tag{3.1}$$

We distinguish two cases: $p \leq T_a$ and $p > T_a$.

*Case 1:* If $p \leq T_a$, then (3.1) becomes

$$p = \alpha p + (1 - \alpha) \min\left\{T_j, f(p)\right\},$$

which, since $\alpha < 1$, is equivalent to

$$p = \min\left\{T_j, f(p)\right\}.$$

This equation has a solution $p \leq T_a$ if and only if $p = 1 \leq \min\{T_a, T_j\}$ or $p = T_j \leq \min\{T_a, 1\}$. Hence, statements (i) and (ii) are proved.

*Case 2:* If $p > T_a$, then (3.1) becomes

$$p = \alpha T_a + (1 - \alpha) \min\left\{T_j, f(T_a)\right\}.$$

Accordingly, there exists a solution $p \geq T_a$ if and only if $T_a \leq \min\{T_j, f(T_a)\}$. By (H1), $T_a \leq f(T_a)$ holds if and only if $T_a \leq 1$, and therefore a solution $p \geq T_a$ exists if and only if $T_a \leq \min\{T_j, 1\}$; leading to (iii). □

In the particular cases when only one of the age classes is targeted, we have the following corollaries. Notice that in case of juvenile-only harvest, we can assume that $T_a$ is large enough so that $T_a > \max\{T_j, 1\}$, and in case of adult-only harvest, we can assume that $T_j$ is large enough so that $T_j > \max\{T_a, 1, f(T_a)\}$.

**Corollary 3.2.** *Assume* (H1). *Then model (JH) given by* (2.5) *has a unique positive equilibrium p, which is:*

(i) $p = 1$, *if* $T_j \geq 1$;
(ii) $p = T_j$, *if* $T_j \leq 1$.

**Corollary 3.3.** *Assume* (H1). *Then model (AH) given by* (2.6) *has a unique positive equilibrium p, which is:*

(i) $p = 1$, *if* $T_a \geq 1$;
(ii) $p = \alpha T_a + (1 - \alpha)f(T_a)$, *if* $T_a \leq 1$.

Next, we investigate equilibria stability properties of Eqs. (2.5)–(2.7). For it, we introduce the auxiliary second-order difference equation

$$x_{n+1} = g(x_{n-1}, x_n), \tag{3.2}$$

where $g : (0, +\infty) \times (0, +\infty) \to [0, +\infty)$ is a continuous map.

We say that a positive equilibrium $p$ of (3.2) is a *stable attractor* (briefly, LAS) if for every neighborhood $U$ of $p$ there is a neighborhood $V$ of $p$ such that every solution $(x_n)_{n \in \mathbb{N}}$ is included in $U$ and

$$\lim_{n \to \infty} x_n = p, \tag{3.3}$$

provided that $\{x_0, x_1\} \subset V$. Moreover, we say that a stable attractor $p$ is a *globally stable attractor* (briefly, GAS) if (3.3) holds for all solutions $(x_n)_{n \in \mathbb{N}}$ of (3.2) with positive initial conditions $(x_0, x_1)$.

We now recall a useful result that provides sufficient conditions for equilibria of (3.2) to be globally attracting (cf., [23, Theorem C]). In our framework, we can state it as follows.

**Theorem 3.4** ([23]). *Assume that there exists a continuous map $\varphi : (0, +\infty) \to (0, +\infty)$ satisfying:*

(NF) *negative feedback condition, i.e., there is $p > 0$ such that $(\varphi(x) - x)(x - p) < 0$ for all $x \neq p$;*
(DC) *dominance condition, i.e., if $g(u_0, u_1) \geq \max\{u_0, u_1\}$ (resp., $g(u_0, u_1) \leq \min\{u_0, u_1\}$), then $g(u_0, u_1) \leq \varphi(x)$ (resp., $g(u_0, u_1) \geq \varphi(x))$ for some $x$ in $I := [\min\{u_0, u_1\}, \max\{u_0, u_1\}]$.*

*If p is a global attractor of*

$$x_{n+1} = h(x_n), \tag{3.4}$$

*then p is a globally stable attractor of* (3.2).

For its proof we refer to [23, Theorem C]. Next we state and prove our main result on global stability. It essentially establishes that if the threshold is set at a population level below the positive equilibrium of the unharvested adult population, then the exploited population tends to a positive equilibrium for any initial population sizes, no matter whether the unharvested population is stable or not. Hence, this form of threshold harvesting has a clear stabilizing effect.

Here and later in the paper we employ the usual notation for the second iteration of a one-dimensional map $f$, that is, $f^2(x) := f(f(x))$.

**Theorem 3.5.** *Assume* (H1). *Then the following hold.*

(i)  *If $T_j \leq 1$, then $p = T_j$ is a globally stable attractor of (JH).*
(ii) *If $T_a \leq 1$, then $p = \alpha T_a + (1 - \alpha)f(T_a)$ is a globally stable attractor of (AH).*

*(iii) If $T_a \leq 1$, then $p = \alpha T_a + (1 - \alpha) \min\{T_j, f(T_a)\}$ is a globally stable attractor of (BH) for every fixed $T_j \geq T_a$.*

*(iv) If $T_j \leq 1$, then $p = T_j$ is a globally stable attractor of (BH) for every fixed $T_a \geq T_j$.*

**Proof.** The proof of (*i*) follows by combining [6, Proposition 2.1] and [23, Corollary 4.3]. Indeed, thanks to [6, Proposition 2.1], we deduce that $p_1 = T_j$ is a global attractor of (1.2) provided that $T_j \leq 1$; and so, from [23, Corollary 4.3], we conclude that $p_1$ is a globally stable attractor of (2.5).

To prove (*ii*), we first notice that Eq. (2.6) is a particular case of Eq. (3.2) with $g$ defined by

$$g(u_{n-1}, u_n) = \alpha \min\{u_n, T_a\} + (1 - \alpha)f(\min\{u_{n-1}, T_a\}).$$

We then exploit Theorem 3.4 to prove that $p_2 = \alpha T_a + (1 - \alpha)f(T_a)$ is globally attracting. By (H1), from $T_a \leq 1$, we can infer $f(T_a) \geq T_a$ and hence $p_2 \geq T_a$. Let us define $M_a := \max\{f(x) : x \in [0, T_a]\}$ and $\tilde{p}_2 := \alpha T_a + (1 - \alpha)M_a$, so that we have $\tilde{p}_2 \geq p_2$. Next, we take the non-increasing continuous map $\varphi_2 : (0, +\infty) \to (0, +\infty)$ defined as

$$\varphi_2(x) = \begin{cases} \tilde{p}_2, & \text{if } 0 < x \leq T_a, \\ \tilde{p}_2 + \dfrac{p_2 - \tilde{p}_2}{p_2 - T_a}(x - T_a), & \text{if } T_a < x < p_2, \\ p_2, & \text{if } x \geq p_2. \end{cases}$$

It is clear that the negative feedback condition (NF) of Theorem 3.4 holds for $p = p_2$. Moreover, $p_2$ is a global attractor of $\varphi_2$, since $\varphi_2^2(x) = p_2$, for all $x > 0$. It thus remains to check dominance condition (DC) of Theorem 3.4. To this purpose we divide the proof into two steps.

*Step 1.* If $g(u_0, u_1) \geq \max\{u_0, u_1\}$, then $g(u_0, u_1) \leq \varphi_2(x)$ for some $x \in I$. We distinguish two cases:

- if $u_0 \geq T_a$, then, for every $u_1 > 0$, $g(u_0, u_1) = \alpha \min\{u_1, T_a\} + (1 - \alpha)f(T_a) \leq \alpha T_a + (1 - \alpha)f(T_a) = p_2 \leq \varphi_2(u_0)$;
- if $u_0 < T_a$, then, for every $u_1 > 0$, $g(u_0, u_1) = \alpha \min\{u_1, T_a\} + (1 - \alpha)f(u_0) \leq \alpha T_a + (1 - \alpha)M_a = \tilde{p}_2 = \varphi_2(u_0)$.

Thus (DC) follows in the both cases.

*Step 2.* If $g(u_0, u_1) \leq \min\{u_0, u_1\}$, then $g(u_0, u_1) \geq \varphi_2(x)$ for some $x \in I$. We distinguish four cases:

- if $\min\{u_0, u_1\} \geq T_a$, then $g(u_0, u_1) = \alpha T_a + (1 - \alpha)f(T_a) = p_2 = \varphi_2(u_0)$;
- if $\max\{u_0, u_1\} < T_a$, then $g(u_0, u_1) = \alpha u_1 + (1 - \alpha)f(u_0) > \alpha u_1 + (1 - \alpha)u_0 \geq \min\{u_0, u_1\}$;
- if $u_0 < T_a \leq u_1$, then $g(u_0, u_1) = \alpha T_a + (1 - \alpha)f(u_0) > \alpha T_a + (1 - \alpha)u_0 > u_0$;
- if $u_1 < T_a \leq u_0$, then $g(u_0, u_1) = \alpha u_1 + (1 - \alpha)f(T_a) \geq \alpha u_1 + (1 - \alpha)T_a > u_1$.

Notice that (DC) is proved only in the first case, since $p_2 \geq T_a$ and so $\min\{u_0, u_1\} \geq p_2$. In the remaining three cases, the inequality $g(u_0, u_1) \leq \min\{u_0, u_1\}$ never holds.

To prove (*iii*), we argue as for the proof of statement (*ii*). Eq. (2.7) is a particular case of Eq. (3.2) with $g$ defined by

$$g(u_{n-1}, u_n) = \alpha \min\{u_n, T_a\} + (1 - \alpha) \min\left\{T_j, f\left(\min\{u_{n-1}, T_a\}\right)\right\}. \tag{3.5}$$

As for (*iii*), we introduce the non-increasing continuous map $\varphi_3 : (0, +\infty) \to (0, +\infty)$ defined as follows

$$\varphi_3(x) = \begin{cases} \tilde{p}_3, & \text{if } 0 < x \leq T_a, \\ \tilde{p}_3 + \dfrac{p_3 - \tilde{p}_3}{p_3 - T_a}(x - T_a), & \text{if } T_a < x < p_3, \\ p_3, & \text{if } x \geq p_3, \end{cases}$$

where $p_3 := \alpha T_a + (1 - \alpha) \min\{T_j, f(T_a)\}$ and $\tilde{p}_3 := \alpha T_a + (1 - \alpha) \min\left\{T_j, M_a\right\}$. Notice that $\tilde{p}_3 \geq p_3 \geq T_a$ and $\varphi_3^2(x) = p_3$, for all $x > 0$. Moreover, we can verify conditions (NF) and (DC) of Theorem 3.4 following step-by-step the proof of statement (*ii*). Hence, we obtain that $p_3$ is a globally stable attractor of (2.7).

At last, we prove (*iv*). Notice that Eq. (2.7) reduces to Eq. (3.5) in this case. To apply Theorem 3.4, we define

$$\varphi_4(x) = \begin{cases} T_j, & \text{if } 0 < x \leq T_j, \\ \min\{T_j, f(\min\{x, T_a\})\}, & \text{if } x \geq T_j. \end{cases}$$

As in the previous cases, it is clear that the negative feedback condition (NF) of Theorem 3.4 holds for $p = T_j$. Moreover, $T_j$ is a global attractor of $\varphi_4$, since $\varphi_4^2(x) = T_j$, for all $x > 0$. It thus remains to check dominance condition (DC) of Theorem 3.4. We divide the proof into two steps.

*Step 1.* If $g(u_0, u_1) \geq \max\{u_0, u_1\}$, then $g(u_0, u_1) \leq \varphi_4(x)$ for some $x \in I$. We distinguish three cases:

- if $u_1 > T_j$, then, $g(u_0, u_1) = \alpha \min\{u_1, T_a\} + (1 - \alpha) \min\{T_j, f(\min\{u_0, T_a\})\} \leq \alpha u_1 + (1 - \alpha)T_j < u_1$;
- if $u_1 \leq T_j$ and $u_0 \leq T_j$, then, $g(u_0, u_1) \leq \alpha u_1 + (1 - \alpha)T_j \leq T_j = \varphi_4(u_1)$;
- if $u_1 \leq T_j$ and $u_0 > T_j$, then, $g(u_0, u_1) = \alpha u_1 + (1 - \alpha)\varphi_4(u_0)$, and therefore $g(u_0, u_1) \geq \max\{u_0, u_1\} \geq u_1$ implies that $g(u_0, u_1) \leq \varphi_4(u_0)$.

In the first case, the inequality $g(u_0, u_1) \geq \max\{u_0, u_1\}$ never holds.

*Step 2.* If $g(u_0, u_1) \leq \min\{u_0, u_1\}$, then $g(u_0, u_1) \geq \varphi_4(x)$ for some $x \in I$. We distinguish four cases:

- if $u_0 < T_j$ and $u_1 < T_a$, then, $g(u_0, u_1) = \alpha u_1 + (1 - \alpha) \min\{T_j, f(u_0)\} > \alpha u_1 + (1 - \alpha)u_0 \geq \min\{u_0, u_1\}$;
- if $u_0 < T_j$ and $u_1 \geq T_a$, then $g(u_0, u_1) = \alpha T_a + (1 - \alpha) \min\{T_j, f(u_0)\} > \alpha T_a + (1 - \alpha)u_0 \geq u_0$;
- if $u_0 \geq T_j$ and $u_1 \geq T_j$, then $g(u_0, u_1) = \alpha \min\{u_1, T_a\} + (1 - \alpha)\varphi_4(u_0) \geq \alpha T_j + (1 - \alpha)\varphi_4(u_0) \geq \varphi_4(u_0)$;
- if $u_0 \geq T_j$ and $u_1 < T_j$, then, $g(u_0, u_1) = \alpha u_1 + (1 - \alpha)\varphi_4(u_0)$, and so, if $g(u_0, u_1) \leq \min\{u_0, u_1\} \leq u_1$, then $g(u_0, u_1) \geq \varphi_4(u_0)$.

Notice that the inequality $g(u_0, u_1) \leq \min\{u_0, u_1\}$ never holds in the first two cases of this step, and (DC) follows in the others. The proof is thus completed. □

In Theorem 3.5, we proved that (BH) has a globally stable attractor if $\min\{T_a, T_j\} \leq 1$. In the remaining case, that is, if $\min\{T_a, T_j\} > 1$, we know by Proposition 3.1 that $p = 1$ is the unique positive equilibrium. Our next result shows that if 1 is a global attractor of (1.1), then it is a globally stable attractor of (BH). This generalizes analogous results for one-dimensional models with different forms of threshold harvesting (see [6, Proposition 2.2], [5, Proposition A.3], and [8, Theorem 2]).

**Theorem 3.6.** *Assume* (H1). *If* $\min\{T_a, T_j\} > 1$, *then* $p = 1$ *is the unique positive equilibrium of* (2.7). *Moreover, if* $p$ *is a global attractor of* (1.1), *then* $p$ *is a globally stable attractor of* (2.7).

To prove our next theorem, we are going to use [23, Lemma 2.5 and Theorem B], which we state here below (adapted to our situation for convenience of the reader).

**Lemma 3.7** ([23]). *Assume that there exists a continuous map* $h : (0, +\infty) \to (0, +\infty)$. *If* $p$ *is a global attractor of* (3.4), *then there are no distinct points* $c, d \in (0, +\infty)$ *satisfying* $h(c) \geq \max\{c, d\}$ *and* $h(d) \leq \min\{c, d\}$.

**Theorem 3.8** ([23]). *Assume that* $p$ *is a globally stable attractor of* (1.1) *where* $f : (0, +\infty) \to (0, +\infty)$ *is a continuous map. Suppose there exists a continuous map* $h : (0, +\infty) \to (0, +\infty)$ *satisfying* $x < h(x) \leq \max\{f(x), p\}$ *(resp.,* $x > h(x) \geq \min\{f(x), p\}$) *for every* $x < p$ *(resp., for every* $x > p$). *Then* $p$ *is a globally stable attractor of* (3.4).

**Proof of Theorem 3.6.** We use again Theorem 3.4 and so we consider the non-increasing continuous map $\varphi_5 : (0, +\infty) \to (0, +\infty)$ defined as $\varphi_5(x) = \min\left\{T_j, f\left(\min\{x, T_a\}\right)\right\}$.

It is clear that the negative feedback condition (NF) of Theorem 3.4 holds for $p = 1$. We claim that $p$ is a global attractor of $x_{n+1} = \varphi_5(x_n)$. To this aim, we distinguish two cases:

- If $f(T_a) \geq 1$, then $x < \varphi_5(x) \leq \max\{f(x), 1\}$ for all $x \in (0, 1)$ and $x > \varphi_5(x) \geq \min\{f(x), 1\}$ for all $x > 1$; that is, $\varphi_5$ is dominated by $f$. Thus, by Theorem 3.8, the claim is proved.
- If $f(T_a) < 1$, then we can write

$$\varphi_5(x) = \begin{cases} \min\left\{T_j, f(x)\right\}, & \text{if } x \leq T_a; \\ f(T_a), & \text{if } x \geq T_a. \end{cases}$$

  Since $\varphi_5$ is not necessarily dominated by $f$ for $x > T_a$, we consider the auxiliary function

$$\varphi_a(x) = \begin{cases} \min\left\{T_j, f(x)\right\}, & \text{if } x \leq T_a; \\ f(x), & \text{if } x \geq T_a. \end{cases}$$

  It is easy to check that $\varphi_a$ is dominated by $f$ in the sense of Theorem 3.8. Thus, $p = 1$ is a globally stable attractor of $x_{n+1} = \varphi_a(x_n)$. In particular, this equation does not have 2-periodic points other than $p$; moreover, by Lemma 3.7, $\varphi_a^2(T_a) < T_a$ (take $d = T_a$, $c = \varphi_a(T_a)$ in the lemma). Hence, since $\varphi_5^2(T_a) = \varphi_a^2(T_a) < T_a$, it follows that $\varphi_5^2(x) < x$ for all $x > T_a$. Therefore, $\varphi_5$ cannot have 2-periodic points different from $p$, and so the claim is proved also in this case (see, e.g., [28, Proposition 1]).

It remains to check dominance condition (DC) of Theorem 3.4. We divide the proof into two steps. Recall that

$$g(u_0, u_1) = \alpha \min\{u_1, T_a\} + (1 - \alpha) \min\left\{T_j, f\left(\min\{u_0, T_a\}\right)\right\}.$$

*Step 1.* If $g(u_0, u_1) \geq \max\{u_0, u_1\}$, then $g(u_0, u_1) \leq h(x)$ for some $x \in I = [\min\{u_0, u_1\}, \max\{u_0, u_1\}]$. Indeed, $u_1 \leq g(u_0, u_1) \leq \alpha u_1 + (1 - \alpha)h(u_0)$ implies that $h(u_0) \geq g(u_0, u_1)$.

*Step 2.* If $g(u_0, u_1) \leq \min\{u_0, u_1\}$, then $g(u_0, u_1) \geq h(x)$ for some $x \in I$. We distinguish three cases:

- if $u_1 \leq T_a$, then $u_1 \geq g(u_0, u_1) = \alpha u_1 + (1 - \alpha)h(u_0)$, which implies $h(u_0) \leq g(u_0, u_1)$;
- if $g(u_0, u_1) \leq T_a < u_1$, then $T_a \geq g(u_0, u_1) = \alpha T_a + (1 - \alpha)h(u_0)$ which implies $h(u_0) \leq g(u_0, u_1)$:
- finally, we show that $T_a < g(u_0, u_1) \leq \min\{u_0, u_1\}$ is not possible; indeed, if $T_a < \min\{u_0, u_1\}$, then

$$h(u_0) = \min\left\{T_j, f(T_a)\right\} \leq f(T_a) < T_a \Longrightarrow g(u_0, u_1) = \alpha T_a + (1 - \alpha)h(u_0) < T_a,$$

  a contradiction. □

**Remark 3.9.** Let $f$ be the Ricker map defined in (2.1). It is well known that $p = 1$ is a global attractor of (1.1) if $r \leq 2$. Hence, in this case, by an application of Theorems 3.5 and 3.6, it follows that (BH) has always a globally stable attractor $p > 0$, that can be $p = 1$, $p = T_j$, or $p = \alpha T_a + (1 - \alpha) \min\{T_j, f(T_a)\}$.

## 4. Hydra effects

In this section, we are interested in *hydra effects for adult population of* (2.3) *and only in the case of stable populations.* They thus occur when a stable positive equilibrium increases as a result of decreasing the thresholds. It is well known that, for population models with overcompensatory density-dependent regulation (e.g., with the Ricker map (2.1)), hydra effects are often observed if recruits (juveniles) are censused, but are hidden when parent stock (adults) is measured (for more discussions, see [13]). For this reason, we focus our study on hydra effects for the adult population. Moreover, we think that this is the most interesting case from the perspective of fisheries, which usually are focused on adult population stock.

The existence of hydra effects in the adult population has been investigated in [19,21] when proportional harvesting is applied to (2.3), namely $h_a(x) = (1 - \gamma_a)x$ and $h_j(x) = (1 - \gamma_j)x$, with $\gamma_a$ and $\gamma_j$ in [0, 1]. In particular, for overcompensatory models, hydra effects were observed in the case of adult-only harvesting, but not when only juveniles are harvested or both stages are harvested in equal proportion. On the contrary, for compensatory maps (e.g., with the Beverton–Holt map $f(x) = k_1 x/(1 + k_2 x)$, $k_1, k_2 > 0$) hydra effects were not possible.

We now show that analogous conclusions hold in our models with threshold harvesting. From Proposition 3.1, it is clear that hydra effects are not possible if $f$ is increasing, that is, for compensatory models. Thus, in this section, we consider overcompensatory models by assuming that $f$ is unimodal with one local extremum point in (0, 1). Indeed, if this point exceeds the value 1, then one can show that the equilibrium of the adult population keeps increasing as the threshold parameter $T_a$ increases, so hydra effects never occur as for compensatory models. It is also clear from a biological point of view that a hydra effect in adults does not make sense when only juveniles are harvested (mathematically, this is also clear from Corollary 3.2). We thus investigate the impact of threshold harvesting on the hydra effects on the adult population when only adults are harvested, and when both age classes are harvested, considering different thresholds for each stage. The hypotheses required in our next result are typical for the usual discrete maps employed in overcompensatory population models, including the Ricker map, the quadratic map, and the generalized Beverton–Holt map $f(x) = ax/(1 + (a - 1)x^m)$, $a > 1$, $m > 1$.

**Theorem 4.1.** *Assume* (H1). *Suppose that $f$ is of class $C^2$ and has a unique critical point $x_c \in (0, 1)$ such that $f'(x) > 0$ and $f''(x) < 0$ for every $x \in (0, x_c)$, and $f'(x) < 0$ for every $x \in (x_c, +\infty)$. Moreover, $f$ has at most one inflection point $x_m \in (x_c, \infty)$. Then the following hold.*

(i) *A hydra effect as $T_a$ decreases from $T_a = 1$ to $T_a = 0$ occurs in* (AH) *if and only if $\alpha < \alpha_1^*$ where the constant $\alpha_1^* = \alpha_1^*(f) \in (0, 1)$.*

(ii) *A hydra effect as $T_a$ decreases from $T_a = 1$ to $T_a = 0$ occurs in* (BH) *if and only if $T_j > 1$ and $\alpha < \alpha_2^*$ where the constant $\alpha_2^* = \alpha_2^*(f, T_j) \in (0, 1)$.*

*In both cases, a hydra effect cannot occur as $T_a$ decreases while $T_a \geq 1$. In* (ii), *a hydra effect cannot occur as $T_j$ decreases for any fixed value of $T_a$.*

**Proof.** As for statement (i), we use Corollary 3.3 and deal with (2.6). Indeed, we notice that a hydra effect can only occur if $T_a < 1$, since the equilibrium is constant for $T_a \geq 1$. In this case, the positive equilibrium is $p = \alpha T_a + (1 - \alpha)f(T_a)$ and so we stress that a hydra effect may exist only if $f$ is decreasing in $T_a$ (otherwise, the equilibrium is an increasing function of $T_a$). We thus investigate the monotonicity of the function $F(x) := \alpha x + (1 - \alpha)f(x)$ in the interval [0, 1]; by claiming that there exists $\bar{x} \in (0, 1]$ such that

$$F'(\bar{x}) < 0. \tag{4.1}$$

Since $f'(x) \geq 0$ for every $x \in [0, x_c]$, we can infer that $\bar{x}$ (if it exists) has to belong to $(x_c, 1]$. The function $F'$ attains its global minimum over $(x_c, 1]$ at $\bar{x} = 1$ (if $x_m \geq 1$) or at $\bar{x} = x_m$ (if $x_m < 1$). Then, by defining

$$\alpha_1^* = \alpha_1^*(f) := \begin{cases} \dfrac{-f'(1)}{1 - f'(1)}, & \text{if } x_m \geq 1; \\ \dfrac{-f'(x_m)}{1 - f'(x_m)}, & \text{otherwise}; \end{cases} \tag{4.2}$$

we obtain that (4.1) holds if and only if $\alpha < \alpha_1^*$ and so the statement is proved.

To prove statement (ii), we use Proposition 3.1 and deal with (2.7). Therefore, a hydra effect can only occur if $T_a < \min\{T_j, 1\}$. In this case, the positive equilibrium is

$$p = \alpha T_a + (1 - \alpha) \min\{T_j, f(T_a)\} = \begin{cases} \alpha T_a + (1 - \alpha)T_j, & \text{if } T_j \leq f(T_a); \\ \alpha T_a + (1 - \alpha)f(T_a), & \text{if } T_j > f(T_a). \end{cases}$$
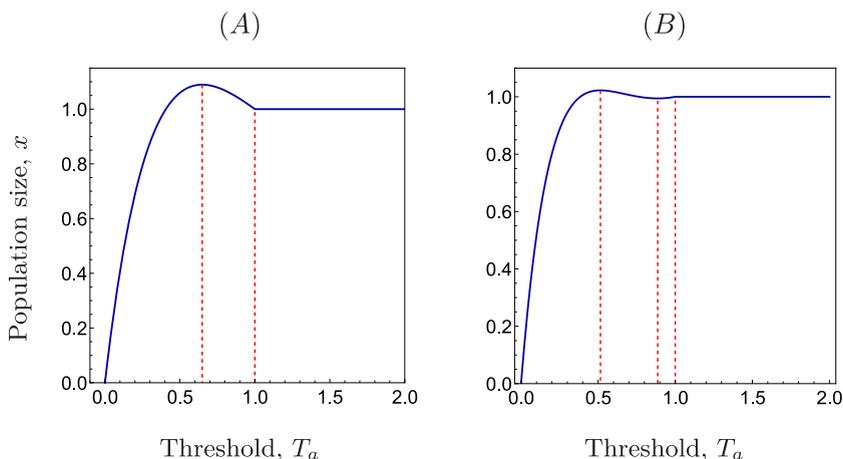
**Fig. 1.** Positive equilibrium for (AH) with $f(x) = xe^{r(1-x)}$. From the right to the left, red dashed lines correspond to $T_a = 1$ and $T_a = v_j$, where $v_j$ are the solutions of $F'(T_a) = 0$ in $(0, 1)$ and $F(x) = \alpha x + (1 - \alpha)f(x)$. (A): $r = 1.75$, $\alpha = 0.2 < (r - 1)/r = 3/7$; a hydra effect occurs as $T_a$ decreases from $T_a = 1$ to $T_a = v_1 \approx 0.648$; (B): $r = 3$, $\alpha = 0.7$, with $(r - 1)/r = 2/3 < \alpha < e^{r-2}/(1 + e^{r-2}) \approx 0.731$; a hydra effect occurs as $T_a$ decreases from $T_a = v_2 \approx 0.886$ to $T_a = v_1 \approx 0.514$.

It thus follows that a hydra effect is only possible if $T_j > f(T_a)$ and there is $\bar{x} \in (0, 1]$ satisfying (4.1). To this purpose, we notice that for every $T_j \in (0, f(x_c))$ there are $\beta_1 \in (0, x_c)$ and $\beta_2 \in (x_c, +\infty)$ such that $T_j = f(\beta_1) = f(\beta_2)$. Then, no hydra effect occur when $T_j = f(\beta_2) < 1$ (or equivalently $\beta_2 > 1$) since the equilibrium is an increasing function of $T_a$. On the other hand, when $T_j = f(\beta_2) > 1$, we define

$$\alpha_2^* = \alpha_2^*(f, T_j) := \begin{cases} \dfrac{-f'(1)}{1 - f'(1)}, & \text{if } x_m \geq 1; \\[2mm] \dfrac{-f'(x_m)}{1 - f'(x_m)}, & \text{if } \beta_2 \leq x_m < 1; \\[2mm] \dfrac{-f'(\beta_2)}{1 - f'(\beta_2)}, & \text{if } x_m < \beta_2 < 1. \end{cases} \tag{4.3}$$

Similarly to the previous case, we have that (4.1) holds if and only if $\alpha < \alpha_2^*$.

The proof of Theorem 4.1 is thus completed. □

**Remark 4.2.** It is easy to check that $\alpha_2^* = \alpha_2^*(f, T_j)$ is a nonincreasing function of $T_j$. Hence, since $\alpha_1^* = \alpha_1^*(f)$ can be seen as $\alpha_2^*(f, \infty)$, we can affirm that $\alpha_1^* \geq \alpha_2^*$.

In Theorem 4.1, we proved that when only adults are harvested may give rise to a hydra effect in the adult population in (AH). As for the general case (BH), we show that a hydra effect in the adult population can occur provided that $0 < T_a < 1 < T_j$, that is, if juveniles are more protected than adults. It is worth mentioning that it was shown that hydra effects do not occur in (2.2) if proportional harvesting is applied with the same harvesting rates in juveniles and adults [21, Proposition 2.5]. The same occurs for threshold harvesting, but our results show that hydra effects are still possible if both age classes are targeted, but harvesting intensity is greater for adult population.

**Example 4.3.** Let $f$ be the Ricker map defined in (2.1). In this case, we can make explicit computations of the threshold values $\alpha_1^*$ and $\alpha_2^*$ defined in (4.2) and (4.3), respectively. We first observe that the map $x \mapsto -f'(x)/(1 - f'(x))$ is a strictly decreasing function in $[0, 1]$ if and only if $2/r \geq 1$, otherwise it has there a local minimum at $x_m = 2/r$. Then, from Theorem 4.1 and by considering the Lambert function $W_{-1} : [-1/e, 0) \to (-\infty, -1]$, which is the lower branch of the inverse of $\phi(x) = xe^x$, we have the following cases:

- $\alpha < \alpha_1^*$ if and only if either $1 < r \leq 2$ and $\alpha < \dfrac{r - 1}{r}$, or $r > 2$ and $\alpha < \dfrac{e^{r-2}}{1 + e^{r-2}}$.

- $\alpha < \alpha_2^*$ if and only if either $1 < r \leq 2$ and $\alpha < \dfrac{r - 1}{r}$, or $r > 2/\beta_2$ and $\alpha < \dfrac{-f'(\beta_2)}{1 - f'(\beta_2)}$, or $2 < r \leq 2/\beta_2$ and

  $\alpha < \dfrac{e^{r-2}}{1 + e^{r-2}}$, where $\beta_2 = \dfrac{-1}{r} W_{-1}(-T_j r e^{-r})$.

See Figs. 1 and 2 for some numerical simulations and a graphical representation of these cases. In Fig. 1, we show two panels, illustrating the two different possibilities for $\alpha_1^*$: panel (A) corresponds to the case $1 < r \leq 2$ ($x_m \geq 1$), and panel
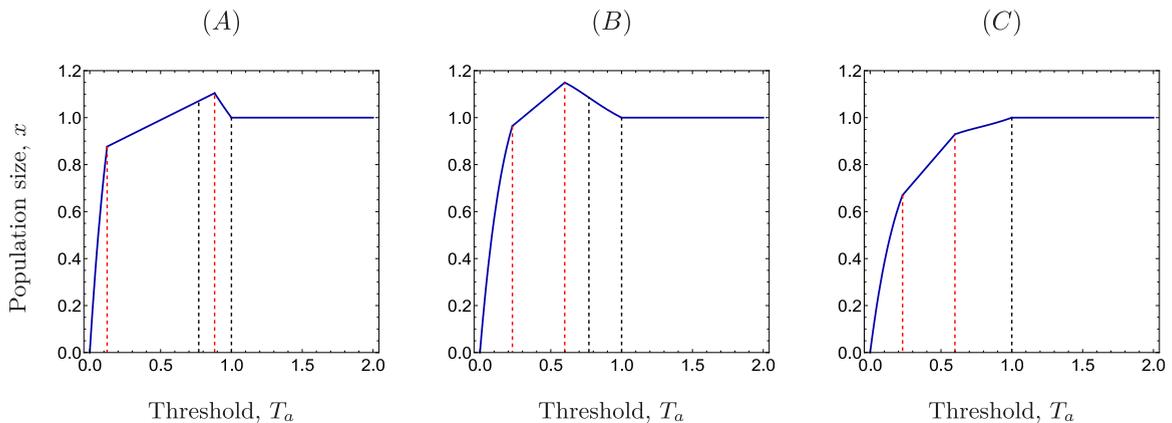
**Fig. 2.** Positive equilibrium for (BH) with $f(x) = xe^{2.6(1-x)}$. From the left to the right, red dashed lines correspond to $T_a = \beta_1$ and $T_a = \beta_2$, while black dashed lines correspond to $T_a = x_m = 2/r < 1$ (panels (A) and (B)) and $T_a = 1$ (all panels). (A): $T_j = 1.2$, where $x_m < \beta_2 < 1$; a hydra effect occurs for $\alpha = 0.3 < -f'(\beta_2)/\left(1 - f'(\beta_2)\right) \approx 0.63$ as $T_a$ decreases from 1 to $\beta_2$; (B): $T_j = 1.7$, where $\beta_2 < x_m < 1$; a hydra effect as $T_a$ decreases from 1 to $\beta_2$ occurs for $\alpha = 0.5 < \alpha_2^* = e^{0.6}/(1 + e^{0.6}) \approx 0.64$; (C): $T_j = 1.7$ and $\alpha = 0.7 > \alpha_2^*$, hence the equilibrium always decreases as $T_a$ decreases from 1 to 0.

(B) corresponds to the case $r > 2$ ($x_m < 1$). In Fig. 2, we illustrate the second and third cases of $\alpha_2^*$, and one situation where hydra effect does not occur.

## 5. Bifurcation analysis

To understand the dynamics of models (JH), (AH) and (BH) when the positive equilibrium is unstable in presence of harvesting, we discuss the case of semelparous and iteroparous populations separately. Moreover, for the sake of exposition, we consider, in the following, the Ricker map (2.1) as stock-recruitment function and observe that results can be generalized to other smooth unimodal maps.

### 5.1. Semelparous case: the role of harvesting thresholds

When the population is semelparous, the individuals have only one reproductive event before death, and so $\alpha = 0$. This leads us to deal with models described through a second-order difference equation $A_{n+1} = g(A_{n-1})$, which is a particular case of (3.2). As observed in [29,30], the dynamics of this kind of equation depend on the dynamics of an associated one-dimensional equation $A_{n+1} = g(A_n)$ that is the core of the investigations in this section. For (2.5), we consider the equation

$$A_{n+1} = \min\{f(A_n), T_j\} =: g_1(A_n), \tag{5.1}$$

which corresponds to the threshold harvesting (TH) model studied in [6]. For (2.6), we consider the equation

$$A_{n+1} = f\left(\min\{A_n, T_a\}\right) =: g_2(A_n), \tag{5.2}$$

which is dynamically equivalent to (2.6), but with different census timing [13, Section 5]. From Fig. 3, we observe that the maps $g_1$ and $g_2$ are piecewise smooth maps with one flat interval each one which has a stabilizing effect (see [6]).

On the other hand, for (2.7), we take the equation

$$A_{n+1} = \min\left\{T_j, f\left(\min\{A_n, T_a\}\right)\right\} =: g_3(A_n), \tag{5.3}$$

where the piecewise smooth map $g_3$ has typically two flat intervals as depicted in Fig. 3. In fact, $g_3$ can be written in an extended form as follows:

$$g_3(x) = \begin{cases} f(x), & \text{if } x \le T_a \text{ and } f(x) \le T_j; \\ f(T_a), & \text{if } x > T_a \text{ and } f(T_a) < T_j; \\ T_j, & \text{otherwise.} \end{cases} \tag{5.4}$$

It is worth noticing that Eq. (5.3) has an independent interest as a one-dimensional harvesting model generalizing the two threshold harvesting models (5.1) and (5.2). We can interpret it in the following way: before reproduction, we apply
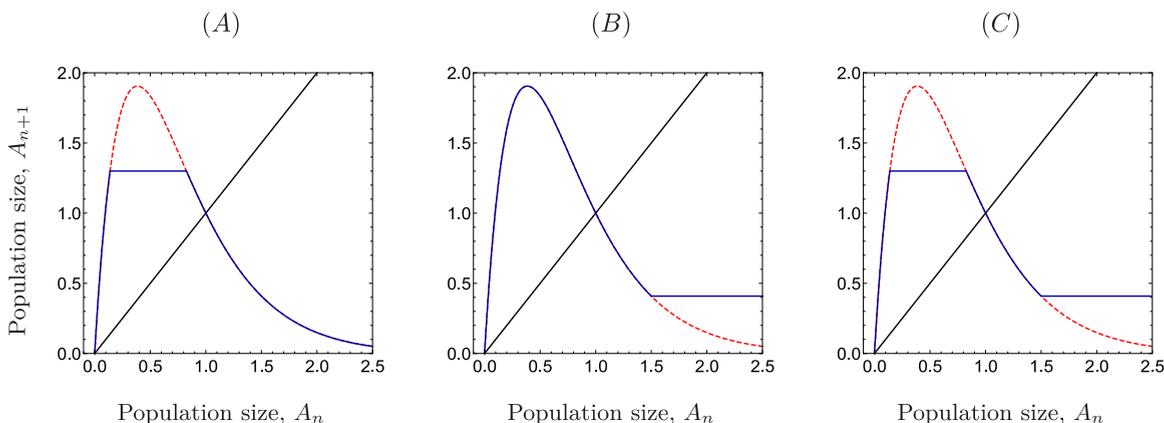
**Fig. 3.** One-dimensional maps defining the different harvest strategies in the semelparous case. Here, the map $f(x) = xe^{2.6(1-x)}$ is represented with a red dashed line in the intervals where it does not coincide with the map $g_i$, $i = 1, 2, 3$ (blue solid line). (*A*): map $g_1$ defined in (5.1) with $T_j = 1.3$; (*B*): map $g_2$ defined in (5.2) with $T_a = 1.5$, $f(T_a) \approx 0.408$; (*C*): map $g_3$ defined in (5.3) with $T_a = 1.5$, $T_j = 1.3$.

threshold harvesting to the population with the threshold $T_a$, then reproduction occurs and we apply again threshold harvesting with the threshold $T_j$, as the following scheme shows

$$\boxed{A_n} \xrightarrow{\text{TH }(T_a)} \boxed{A_n' = \min\{A_n, T_a\}} \xrightarrow{\text{Rep.}} \boxed{f(A_n')} \xrightarrow{\text{TH }(T_j)} \boxed{A_{n+1} = \min\{f(A_n'), T_j\}}$$
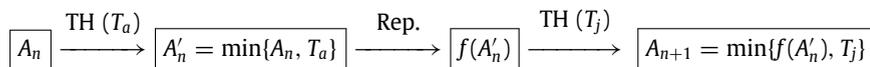
We now perform a bifurcation analysis of (5.3). To this purpose, we follow [10] for notations and results involving piecewise-smooth maps. We thus call *break points* the points where $g_3$ is not differentiable. Moreover, a fixed point of $g_3$ is called *admissible fixed point*; whereas a *virtual fixed point* is a fixed point of one of the smooth maps defining $g_3$ but not a fixed point of $g_3$. For example, $T_j$ and $f(T_a)$ are either virtual or admissible fixed points of $g_3$. Indeed, according to Proposition 3.1, $T_j$ is admissible if and only if either $T_j \leq 1 \leq T_a$, or $T_a < 1$ and $T_j \leq f(T_a)$. Instead, $f(T_a)$ is admissible if and only if $T_a \leq 1$ and $T_j \geq f(T_a)$. Finally, the positive fixed point $p = 1$ of $f$ is admissible if and only if $1 \leq \min\{T_a, T_j\}$.

Here, by varying the threshold parameter $T_j$ or $T_a$ in Eq. (5.3), we are interested in studying when a virtual/admissible fixed point or a cycle collides with a break point, and this collision leads to a qualitative change in the dynamics. This phenomena is called border-collision bifurcations (BCB, for short). There are two possible dynamical scenarios at a BCB defined by a fixed point of $g_3$:

- A *persistence BCB* occurs when an admissible and a virtual fixed point collide at a break point and interchange their roles. No other periodic points are created or destroyed at the bifurcation point.
- A *flip BCB* or *period-doubling BCB* occurs when an admissible fixed point collides with a break point and a 2-periodic orbit $\{q_1, q_2\}$ appears, where $q_1$ and $q_2$ are at different sides of the break point.

We now consider the Ricker map (2.1) and point out that the conclusions for BCBs of fixed points remain valid for any smooth unimodal map satisfying (H1) and such that $f'(1) < 0$. First, we notice that, if $r \leq 2$, then the positive equilibrium $p = 1$ is a global attractor of $f$, and therefore, it is also a global attractor for the threshold methods considered in this section if $\min\{T_a, T_j\} > 1$. Indeed, for (5.1) and (5.2), this is a consequence of [6, Proposition 2.2], while for (5.3), it is a by-product of the proof of Theorem 3.6 in this paper. Thus, for $r \leq 2$, only persistence BCBs occur as either $T_a$ or $T_j$ are increased. Actually, Theorem 3.6 guarantees that the same conclusion is valid for the general model (2.7).

Next, as a case study, we choose $r = 2.6$ in (2.1), so that the corresponding Ricker map $f$ has a 4-periodic attractor. It is easy to check that a persistence BCB occurs when $T_j = f(T_a)$ and $0 < T_a < 1$. The bifurcation boundary in the plane $(T_a, T_j)$ is represented by a blue solid line in Fig. 4.

When $T_j > 1$, a flip BCB occurs as $T_a$ is increased and reaches the critical value $T_a = 1$. For $T_a < 1$, the fixed point $f(T_a)$ is globally attracting; at $T_a = 1$, it collides with a break point and becomes virtual; for $T_a > 1$, the attracting 2-periodic orbit $\{f(T_a), f^2(T_a)\}$ is created. In a similar way, when $T_a > 1$, a flip BCB occurs as $T_j$ is increased and reaches the critical value $T_j = 1$. In this case, the fixed point $T_j$ becomes virtual and gives rise to an attracting 2-periodic orbit $\{T_j, f(T_j)\}$. Flip BCBs are represented by red solid lines in Fig. 4.

BCBs of 2-periodic cycles occur when a fixed point of $g_3^2$ collides with a break point. We find two persistence BCBs and two flip BCBs of 2-periodic cycles. To this aim, let us consider

$$q := \max\{x \in (0, +\infty) : f^2(x) = x\}.$$

Then, $\{q, f(q)\}$ is an (unstable) 2-cycle of $f$. Flip BCBs of 2-periodic cycles occur when either $T_j > q$ and $T_a$ passes the critical value $T_a = q$, or $T_a > q$ and $T_j$ passes the critical value $T_j = q$. In both cases an attracting 2-cycle of $g_3$ becomes virtual
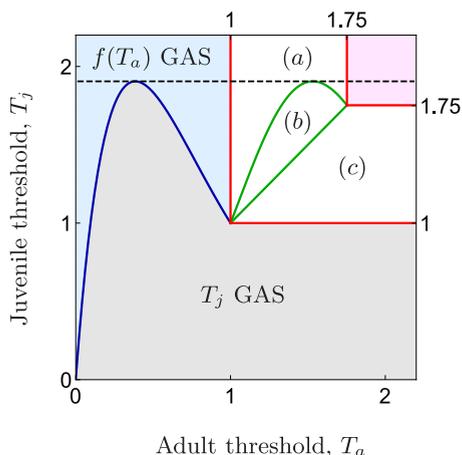
**Fig. 4.** In the plane $(T_a, T_j)$, a bifurcation diagram for (5.3) with $f(x) = xe^{2.6(1-x)}$. When $\min\{T_a, T_j\} \leq 1$, there is a globally attracting positive equilibrium ($T_j$ in the gray region and $f(T_a)$ in the blue region); if $1 < \max\{T_a, T_j\}$ and $\min\{T_a, T_j\} \leq q \approx 1.752$, then there is a globally attracting 2-cycle (white region), which is $\{f(T_a), f^2(T_a)\}$ in region $(a)$, $\{f(T_a), T_j\}$ in region $(b)$, and $\{f(T_j), T_j\}$ in region $(c)$; at last, if $\max\{T_a, T_j\} > q$ (magenta region), there is a 4-periodic attractor. We show: flip BCBs in red solid line; persistence BCBs for fixed points in blue solid line; persistence BCBs for 2-cycles in green solid line. If $T_j > M = \max\{f(x) : x \in [0, 1]\} \approx 1.905$ (the region above the horizontal dashed line), then (5.3) reduces to (5.2), and we have the typical period-doubling bifurcation sequence of TH as $T_a$ is increased; an analogous comment applies for $T_j$ when $T_a > q$.
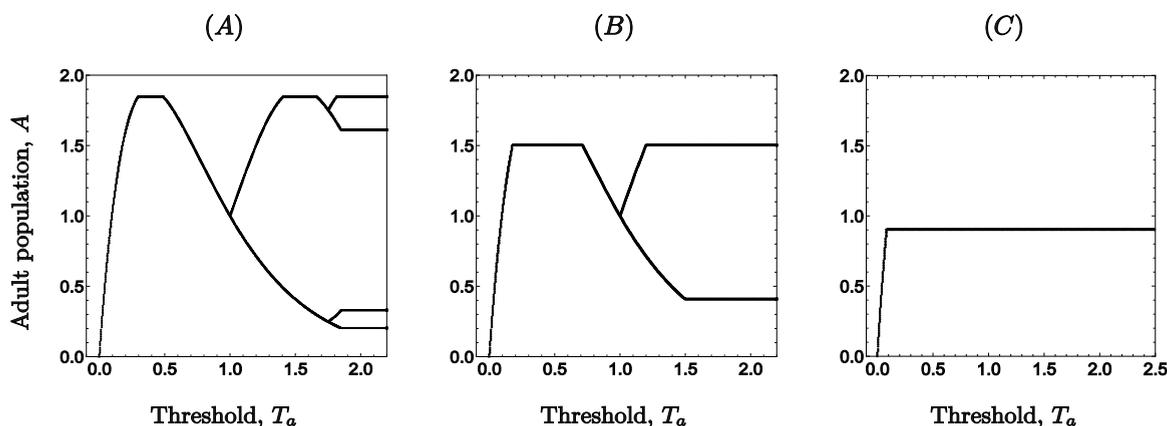


**Fig. 5.** One-parameter bifurcation diagrams for (5.3) with $f(x) = xe^{2.6(1-x)}$. We use $T_a$ as the bifurcation parameter and fix different values of $T_j$. $(A)$: $T_j = 1.85 > q \approx 1.752$; $(B)$: $T_j = 1.5 \in (1, q)$; $(C)$: $T_j = 0.9 < 1$.

and a 4-periodic orbit is created. Persistence BCBs of 2-periodic cycles occur when $1 < T_a < q$ and either $T_j = f^2(T_a)$ or $T_j = T_a$. In the former case, the 2-periodic orbits $\{T_j, f(T_a)\}$ and $\{f(T_a), f^2(T_a)\}$ collide and interchange their roles (between virtual and admissible 2-cycles); in the latter case, $\{T_j, f(T_a)\}$ collides with $\{T_j, f(T_j)\}$. Persistence BCBs of 2-periodic cycles are represented by green solid lines in Fig. 4.

No more flip BCBs occur. In the magenta shaded region in the right upper corner of Fig. 4, there are several persistence BCBs of 4-periodic orbits, but we skip the details. An important consequence of our analysis of the semelparous case is the stabilizing effect of increasing harvesting (by decreasing $T_a$, $T_j$, or both). To further illustrate these effects and the BCBs, we show some one-parameter bifurcation diagrams in Fig. 5.

From the bifurcation analysis performed for (5.3), we are now ready to deal with the second-order equation

$$A_{n+1} = \min\left\{T_j, f\left(\min\{A_{n-1}, T_a\}\right)\right\} = g_3(A_{n-1}), \tag{5.5}$$

which corresponds to (2.7) with $\alpha = 0$. It is easy to describe the periodic orbits of (5.5) in terms of the ones of (5.3) in our case study. For the general case, we refer to [29,30].

- If (5.3) has a globally attracting fixed point $p$, then $p$ is also a global attractor of (5.5).
- If (5.3) has an unstable fixed point $p$ and an attracting 2-cycle $\{q_1, q_2\}$, then (5.5) has an unstable fixed point $p$, an attracting 4-cycle $\{q_1, q_1, q_2, q_2\}$, and another 4-cycle (saddle) $\{q_1, p, q_2, p\}$.
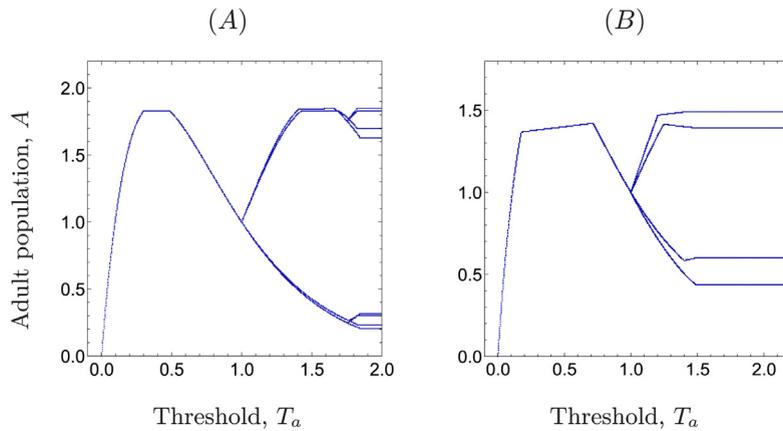
**Fig. 6.** Bifurcation diagrams for (BH) with $f(x) = xe^{2.6(1-x)}$. We use $T_a$ as the bifurcation parameter and fix different values of $\alpha$ and $T_j$. (A): $T_j = 1.85$, $\alpha = 0.015$; (B): $T_j = 1.5$, $\alpha = 0.1$.

- If (5.3) has an unstable fixed point $p$, an unstable 2-cycle $\{q_1, q_2\}$, and an attracting 4-cycle $\{\ell_1, \ell_2, \ell_3, \ell_4\}$, then (5.5) has an unstable fixed point, two unstable 4-cycles, two attracting 8-cycles and three saddles of period 8. The attractors correspond to the initial conditions $\{\ell_1, \ell_1\}$, and $\{\ell_1, \ell_2\}$.

We call the attention to the fact that bifurcation diagrams like those in Fig. 5 do not change when we replace (5.3) by (5.5). However, we should notice that, in the latter case, a seemingly 2-periodic (resp., 4-periodic) orbit in the bifurcation diagram actually corresponds to a 4-periodic orbit (resp., 8-periodic).

### 5.2. Iteroparous case: the role of adult survivorship rates

Numerical experiments suggest that the configuration of periodic orbits of the semelparous case (5.5) with the Ricker map $f(x) = xe^{2.6(1-x)}$ is preserved for $\alpha$ small enough. For a related analytical result, see [24, Theorem 8]. As commented before, when we consider Eq. (5.5), we get the bifurcation diagrams shown in Fig. 5. However, the periodic attractors are different from those of the one-dimensional case; for example, in Fig. 5(B) the apparently 2-periodic orbits of the form $\{q_1, q_2\}$ are in fact 4-periodic orbits of the form $\{q_1, q_1, q_2, q_2\}$, and a similar remark applies to 4-periodic orbits. When $\alpha > 0$, the periods of the attractors are clearly observed in the bifurcation diagram. In Fig. 6, we highlight this contrast by showing the bifurcation diagrams for positive values of $\alpha$ and the same choices of the parameter $T_j$ made in Fig. 5(A) and (B).

The dynamics of (BH) when $\min\{T_a, T_j\} > 1$ change for larger values of $\alpha$, giving rise to periodic solutions with higher periods and smooth invariant curves. Increasing $\alpha$ is stabilizing in the sense that there is a critical value $\alpha_0$ such that the equilibrium $p = 1$ of (BH) becomes asymptotically stable for $\alpha \in (\alpha_0, 1)$. Notice that the value of $\alpha_0$ corresponds to a Neimark–Sacker bifurcation, and, if $f$ is smooth and $f'(1) < -1$, we have $\alpha_0 = \left(f'(1) + 1\right)/f'(1)$ (see [25] for more details). When $\min\{T_a, T_j\} > 1$ and $A_n, A_{n-1}$ are close to 1, then (2.7) becomes Clark's equation

$$A_{n+1} = \alpha A_n + (1 - \alpha)f(A_{n-1}).$$

For the Ricker map, we thus get $\alpha_0 = (r - 2)/(r - 1)$ (since $f'(1) = 1 - r$).

Next, we pursue the investigations for the case study under consideration which is given by (2.1) with $r = 2.6$. In Fig. 7, we show three bifurcation diagrams for (BH) with the same value of the parameter $T_j$, illustrating different transitions when $T_a$ passes the critical value $T_a = 1$: for $\alpha$ small enough, there is a flip bifurcation from an attracting 4-cycle to a globally stable fixed point, as it occurs in the semelparous case $\alpha = 0$; for larger $\alpha$, but smaller than $\alpha_0$, we observe a Neimark–Sacker bifurcation; finally, for $\alpha > \alpha_0$, there is a persistence BCB, where the fixed points 1 and $p = \alpha T_a + (1 - \alpha)f(T_a)$ collide.

In Fig. 8(B), we give a simple 2-parameter bifurcation diagram in the plane $(T_a, \alpha)$, which roughly shows the stabilizing role of increasing $\alpha$ when $T_a > 1$. In the shaded region, there is a rich dynamics including invariant curves and periodic attractors (see also Fig. 9). Numerical simulations show that, for each $T_a > 1$, there exists $\alpha_1(T_a)$ such that (BH) has a 4-periodic attractor if $0 < \alpha < \alpha_1(T_a)$ (see Fig. 8(A)). Moreover, we define $\alpha_1 := \alpha_1(1^+)$.

Finally, another way to illustrate the role of the parameter $\alpha$ is showing how the attractor of the planar system (2.2) changes as $\alpha$ is increased from $\alpha = 0$. In Fig. 9, we fix values for the TH of adults and juveniles and plot the attractor of (2.2) by varying $\alpha$. We consider several values of $\alpha$ for which different scenarios occur: a 4-periodic orbit, a 17-periodic orbit, a smooth invariant curve, and a fixed point. We emphasize that the dynamical complexity of stage-structured population models with density-dependent regulation has been widely studied in the literature; see, e. g., [31–35].
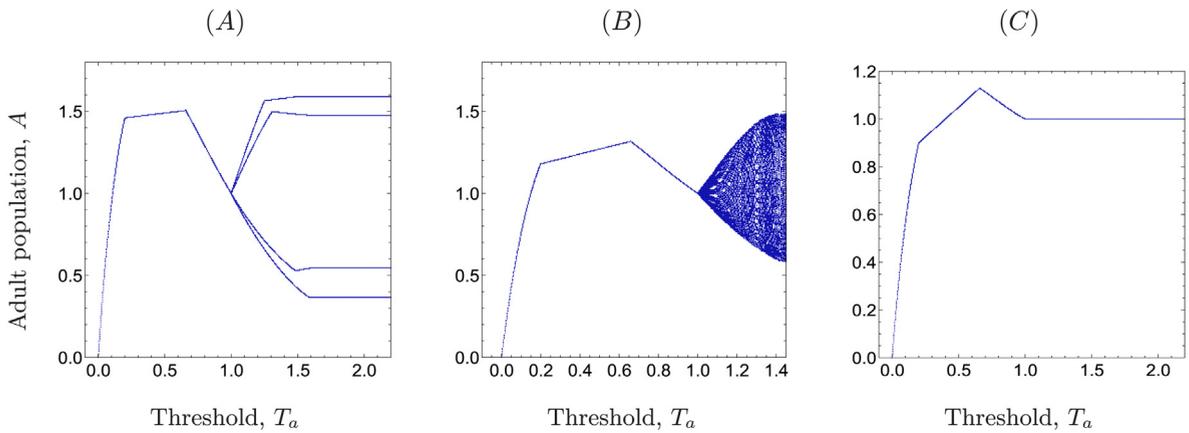
**Fig. 7.** One-parameter bifurcation diagrams for (BH) with the Ricker map $f(x) = xe^{2.6(1-x)}$ and $T_j = 1.6$. We use $T_a$ as the bifurcation parameter and fix different values of $\alpha$. (A): $\alpha = 0.1 < \alpha_1$; (B): $\alpha = 0.3 \in (\alpha_1, \alpha_0)$; (C): $\alpha = 0.5 > \alpha_0$.
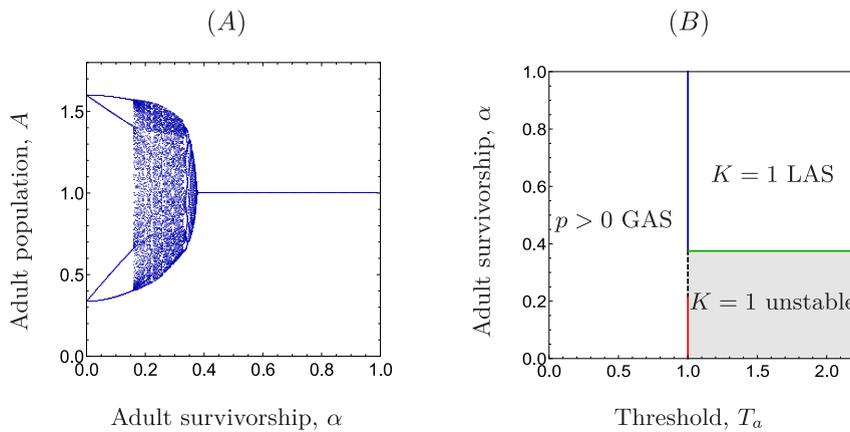


**Fig. 8.** Bifurcation diagrams for (BH) with $f(x) = xe^{2.6(1-x)}$. In this case, $\alpha_0 = (r-2)/(r-1) = 3/8 = 0.375$. (A): 1-parameter bifurcation diagram. We use $\alpha$ as the bifurcation parameter and fix $T_a = 1.8$, $T_j = 1.6$. (B): 2-parameter bifurcation diagram in the plane $(T_a, \alpha)$ when $T_j = 1.6$. We distinguish several bifurcation boundaries: persistence bifurcation in blue solid line, Neimark–Sacker bifurcation in green solid line; flip bifurcation (occurring for $T_a = 1$, $0 < \alpha < \alpha_1 \approx 0.213$) in red solid line.
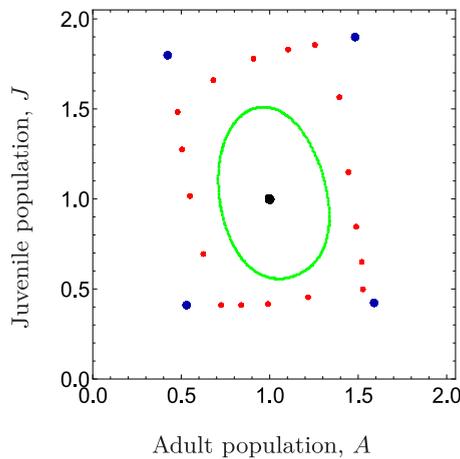


**Fig. 9.** Different attractors of system (2.2) in the plane $(A, J)$, with $f(x) = xe^{2.6(1-x)}$, $T_a = 1.5$, and $T_j = 1.6$: 4-periodic orbit for $\alpha = 0.1$ in blue; 17-periodic orbit for $\alpha = 0.225$ in red; invariant curve for $\alpha = 0.35$ in green; attracting fixed point $(1, 1)$ for $\alpha = 0.5$ in black.

## 6. Discussion

Threshold harvest control rules are considered a key component of the precautionary approach to fisheries management [2]. Our primary aim in this paper was to extend some results recently obtained for one-dimensional single-species populations [4–8] to population models with age-structure. As it has been shown for other forms of harvesting, a demographic structure can confound removal efforts and lead to undesirable consequences. This remark is especially important when, instead of commercial fishing, captures are oriented to pest control, with the aim to eradicate invasive species [19]. A possible effect of fishing or pest control is the so-called hydra effect, which is a form of overcompensation as a response to increasing mortality, and it has been recently argued that this phenomenon is more likely to appear in stage-structured models [17,18]. In this direction, our results indicate that the adult population can increase as a result of threshold harvesting if only adults are harvested, or both juveniles and adults are harvested. In the latter case, a necessary condition for a hydra effect in adult population is that juveniles can only be removed when its population is greater than the equilibrium of the unharvested population. Moreover, we explicitly give the range of parameter values for which hydra effects occur for the Ricker model.

Threshold strategies have also been proposed for stabilizing population dynamics. In this direction, our results in Section 3 rigorously confirm the stabilizing effects of TH in stage-structured populations. We emphasize the use of an enveloping technique introduced in [23] as a successful strategy to prove global stability in difference equations. Moreover, while analyzing the semelparous case in Section 5.1, we introduced a new threshold rule (5.3) for one-dimensional maps, which assumes two reference points $T_j$, $T_a$, depending on whether harvesting is applied before or after reproduction. This rule generalizes the usual limiter control [14,15] and has certain relation with the "both limiter control" introduced by Tung et al. [36]. The bifurcation analysis of this method reveals persistence and flip border-collision bifurcations (BCB), whose analysis provides a 2-parameter bifurcation diagram (in terms of the threshold values $T_a$ and $T_j$) for a case study. Moreover, numerical simulations suggest that these bifurcations persist for the general case when adult survivorship rates are low (see Figs. 6 and 7). Thus, we provide a new example of BCB for non-smooth second-order discrete models.

Finally, we point out that this study aims to be a first step to understand the role of age structure in population models subject to TH. With this respect, we list possible future research directions as follows. On the one hand, we have only considered the case when the survival rates of juveniles and adults are related by equation $s_j = 1 - s_a$. A similar study can be made considering other possibilities; for example, the case $s_a = s_j$ was studied in [19,21] for populations subject to proportional harvesting. On the other hand, it would be interesting to investigate the effects of harvesting in stage-structured models for other threshold strategies, such as proportional threshold harvesting [4,5], precautionary threshold constant catch [8], or threshold constant catch [7].

### CRediT authorship contribution statement

**Eduardo Liz:** Conception and design of study, Writing - original draft, Writing – review & editing. **Elisa Sovrano:** Conception and design of study, Writing - original draft, Writing – review & editing.

### Declaration of competing interest

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

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