

Harvest timing and its population dynamic consequences in a discrete single-species model



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ARTICLE INFO

Article history:

Received 14 May 2013

Received in revised form 5 December 2013

Accepted 10 December 2013

Available online 19 December 2013

Keywords:

Discrete population model

Stability

Constant effort harvesting

Allee effect

Bubbling

Ricker map

ABSTRACT

The timing of harvesting is a key instrument in managing and exploiting biological populations and renewable resources. Yet, there is little theory on harvest timing, and even less is known about the impact of different harvest times on the stability of population dynamics, even though this may drive population variability and risk of extinction. Here, we employ the framework proposed by Seno to study how harvesting at specific moments in the reproductive season affects not only population size but also stability. For populations with overcompensation, intermediate harvest times tend to be stabilizing (by simplifying dynamics in the case of unimodal maps and by preventing bubbling in the case of bimodal maps). For populations with a strong Allee effect, however, intermediate harvest times can have a twofold effect. On the one hand, they facilitate population persistence (if harvesting effort is low). On the other hand, they provoke population extinction (if harvesting effort is high). Early harvesting, currently considered common sense to take advantage of compensatory effects, may cut into the breeding stock when the population has not yet surpassed the critical Allee threshold. The results in this paper highlight, for the first time, the crucial interplay between harvest timing and Allee effects. Moreover, they demonstrate that harvesting with the same effort but at different moments in time can dramatically alter the impact on the population.

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1. Introduction

The sustainable exploitation of natural resources is based on their capability to ‘renew’ themselves [1]. Harvest and management theory is therefore largely concerned with the population response to the removal of individuals or resources [2]. Harvest programmes can differ in their quota or effort, i.e. the number of individuals or proportion of the population taken, but also in their selectiveness by targeting certain spatial areas, sexes, or age and size groups.

A key question of both theoretical and applied interest is the timing of the harvest (or other forms of interventions). For example, marine resources such as fish stocks may be protected from overexploitation by temporary closures of fisheries. In terrestrial ecosystems, large herbivore populations have been expanding across Europe and North America, and they are often managed during specified hunting seasons. Another, particularly illuminating example are species with distinctly seasonal dynamics such as migratory birds, which may be hunted in their wintering or breed-

ing grounds [3]. The management of waterfowl in North America has a long tradition and is well documented in the literature [4–6]. One of the reasons for this research interest is the following: If any management or harvesting programme is to take advantage of population compensation, the timing of interventions relative to density-dependent processes is essential [7,1,2].

A prevailing view and the usual practice in wildlife management is that harvesting should occur after breeding and precede periods of high natural mortality, i.e. early in the autumn [3,8]. This is because the population may compensate the removal of individuals by increased survival (compensatory mortality) or increased productivity (compensatory natality), e.g. due to less competition for resources. Removing individuals early thus improves conditions for the remaining ones and allows them to gain greater reproductive value. Also, in cervid management harvesting juveniles (or males) rather than adult females is considered not only to retain a high yield (and thus population size), but also to dampen the variance in the yield (and thus population variability). However, hunters are often reluctant to shoot juveniles (“hunting Bambi”), and the scientific evidence is scattered (see the review by Milner et al. [9] and references therein).

In the theoretical literature, little is known about the role of harvest timing [10,11,7,3]. The order of harvesting in relation to other events within the life cycle has been shown to profoundly impact the population [12,13,7,3,1,14–16]. This points out

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the potential importance of the harvest *timing*. Yet, we know of only three studies [7,17,18] that allow for variable harvest timings at specific moments in the seasons. The mathematical models in these references are ‘semi-discrete’ in time, that is, they couple continuous processes with discrete events, thus giving rise to hybrid differential equations with periodic or impulsive functions. Moreover, they respectively consider constant yield harvesting, stage structure and environmental fluctuations, which further complicate the models. Here, we employ a simple mathematical model that has been recently proposed by Seno ([19], see also [20,21]). It is based on a single difference equation and yet allows to study the impact of harvest timing.

The Seno model considers constant effort harvesting (sometimes also called proportional harvesting), which is one of the most usual strategies in fisheries [22,23] and pest control [24,19,25]. Many authors have studied the effects of constant effort harvesting on population size in discrete-time models with overcompensatory population dynamics; see, e.g., [26,1,14,13,3,7,27,19,23,25]. Most of these papers focus on the paradoxical increase of population size in response to an increasing mortality (hydra effect) [26,28].

When taking into account the harvest timing, the Seno model predicts that compensatory effects on population size are the larger the earlier the harvesting takes place. It thus arrives at the same conclusion as other models [7,1,3,2]. However, population size is not the only important factor for a sustainable management of an exploited population or for the control of a pest species. Another key point is the stability and degree of complexity of the system; population fluctuations can make the population more prone to extinction by stochastic events, especially in small populations [29].

Although harvesting usually has a stabilizing effect on population dynamics [30,31,13], some recent empirical studies demonstrate the potential for increased mortality to lead to instability in plant, insect and fish populations [32,33,25]. Also, a recent theoretical paper proves that instabilities as a result of increased harvesting effort can be explained in a one-dimensional discrete model without considering external noise or changes in the demographic parameters, if survivorship of adults is allowed [27]. For discrete-time models with dimension higher than one, this phenomenon has been explored too; for example, the three-dimensional model of the flour beetle *Tribolium castaneum* analyzed by Costantino et al. [34], and the two-dimensional model employed by Zipkin et al. [35,25]. In both cases, an increasing adult mortality can destabilize the system. This phenomenon is linked to the mathematical concept of bubbling; for a precise definition, see [27, Definition 3].

An important aspect is whether the stability of the system depends on the harvest timing, and how this dependence affects the qualitative behavior of the population. In this paper, we use Seno’s model to show how the timing of harvesting can affect the stability properties of a population. One of the main conclusions of our study is that an appropriate harvest timing may avoid destabilizing effects in the population, and thus reduce the risk of extinction due to high variability of population size. We also pay special attention to the role of Allee effects, which have been completely ignored so far in this context.

2. The Seno model

Consider a discrete-time single-species population model

$$x_{n+1} = f(x_n) = x_n g(x_n), \tag{2.1}$$

where $x_n \in [0, \infty)$ is the population size at generation $n \in \mathbb{N}$. and $f, g : [0, \infty) \rightarrow \mathbb{R}$ are respectively the population production and the per-capita production. A typical example is the unimodal Ricker

map $f(x) = xe^{r(1-x)}$, with $r > 1$ [36], but we will also allow for survivorship of adults from one generation to the next (giving rise to bimodal maps) and for strong Allee effects (giving rise to multiple equilibria).

We now introduce the harvesting model proposed by Seno (see [19] and references therein). This model assumes that there is a specific season of length one, in which individuals accumulate energy for reproduction. In this paper, we will use this season interchangeably with ‘reproductive season’. Harvesting is assumed to take place at a moment θ ($0 \leq \theta \leq 1$) within the season. Before θ , the population production depends on x_n . Then the harvesting removes a fraction from the population, with $\gamma \in [0, 1)$ being the constant harvesting effort. After θ , the population production depends on $(1 - \gamma)x_n$. The population production is then assumed proportional to the time period before/after harvesting. The model reads (cf. [19, Eq. (1)]):

$$x_{n+1} = (1 - \gamma)x_n(\theta g(x_n) + (1 - \theta)g((1 - \gamma)x_n)). \tag{2.2}$$

Since $f(x) = xg(x)$, we rewrite (2.2) as

$$x_{n+1} = \theta(1 - \gamma)f(x_n) + (1 - \theta)f((1 - \gamma)x_n) := F_\theta(x_n). \tag{2.3}$$

There are two special cases. Firstly, the case $\theta = 0$ means that harvesting occurs at the beginning of the specific season, and then we get $F_0(x) = f((1 - \gamma)x)$; this case has received considerable attention ([26,37,27,23] and references therein). Second, the case $\theta = 1$ gives $F_1(x) = (1 - \gamma)f(x)$. The only difference between the cases $\theta = 0$ and $\theta = 1$ is census timing [14]. Actually, if we agree to measure the population just after reproduction, then the case $\theta = 1$ may be identified with $\theta = 0$. From a mathematical point of view, both cases exhibit the same dynamics because they are topologically conjugated [27]. From a biological point of view, the population dynamics results from the composition of only two separate processes (i.e., harvesting and reproduction), and any difference in population size only depends on when the population is sampled [12].

However, for the mathematical analysis, it is useful to have in mind the case $\theta = 1$ and to realize that every particular choice of F_θ is a convex combination of F_0 and F_1 :

$$F_\theta(x) = \theta F_1(x) + (1 - \theta)F_0(x). \tag{2.4}$$

Our main aim in this paper is to study how the harvesting time parameter θ affects the dynamics of model (2.3).

3. Compensatory models

In this section, we assume that $f(x) = xg(x)$, where g is continuously differentiable and satisfies the following conditions:

- (i) $g'(x) < 0$ for all $x > 0$.
- (ii) $g(0) > 1$.
- (iii) $\lim_{x \rightarrow \infty} g(x) = \delta < 1$.

Conditions (i)–(iii) are typical of single-species models with contest and scramble competition [38] and lead to under- and overcompensating stock–recruitment curves, respectively [22].

Our first observation is that overharvesting provokes extinction. The critical value of the harvesting effort γ is independent of the timing θ .

Proposition 3.1. *Assume that conditions (i)–(iii) hold. Then Eq. (2.3) has a (unique) positive equilibrium if and only if*

$$\gamma < \gamma^* := 1 - \frac{1}{g(0)}. \tag{3.1}$$

If $\gamma \geq \gamma^$, then all solutions of (2.3) converge to zero.*

Proof. Denote $F_\theta(x) = xg_\theta(x)$. Then,

$$g_\theta(x) = \theta(1 - \gamma)g(x) + (1 - \theta)(1 - \gamma)g((1 - \gamma)x).$$

This expression and condition (i) imply that $g'_\theta(x) < 0$ for all $x > 0$. Since

$$\lim_{x \rightarrow \infty} g_\theta(x) = (1 - \gamma)\delta \leq \delta < 1,$$

Eq. (2.3) has a unique positive equilibrium if and only if $g_\theta(0) > 1$, which is equivalent to (3.1).

If $\gamma \geq \gamma^*$ then $F_\theta(x) < x$ for all $x > 0$, and therefore all solutions of (2.3) converge to zero. \square

For example, for the Clark–Ricker map $f(x) = \alpha x + (1 - \alpha)xe^{r(1-x)}$, we have $g(0) = \alpha + (1 - \alpha)e^r$, and therefore

$$\gamma^* = 1 - \frac{1}{\alpha + (1 - \alpha)e^r}.$$

Note that the usual Ricker map corresponds to $\alpha = 0$ and $\gamma^* = 1 - e^{-r}$.

Our next result shows that the size of the positive equilibrium is a monotone function of θ .

Proposition 3.2. Assume that conditions (i)–(iii) hold.

If $0 < \theta_1 < \theta_2 < 1$, then $F_1(x) < F_{\theta_2}(x) < F_{\theta_1}(x) < F_0(x)$ for all $x > 0$ and $\gamma \in (0, 1)$. As a consequence, for a fixed $\gamma < \gamma^*$ the positive equilibrium $K_\gamma(\theta)$ is a decreasing function of $\theta \in [0, 1]$, that is,

$$0 < \theta_1 < \theta_2 < 1 \Rightarrow K_\gamma(0) > K_\gamma(\theta_1) > K_\gamma(\theta_2) > K_\gamma(1). \quad (3.2)$$

Proof. Since $F_0(x) = x(1 - \gamma)g((1 - \gamma)x)$, $F_1(x) = x(1 - \gamma)g(x)$, and g is decreasing, it follows that $F_1(x) < F_0(x)$ for all $x > 0$ and $\gamma \in (0, 1)$. By (2.4), F_θ is a convex combination of F_0 and F_1 , from which it is clear that $F_1(x) < F_{\theta_2}(x) < F_{\theta_1}(x) < F_0(x)$ if $0 < \theta_1 < \theta_2 < 1$.

Next, since $K_\gamma(\theta)$ is the nontrivial intersection of the graph of F_θ and the line $y = x$, the inequalities (3.2) follow immediately. \square

Proposition 3.2 states that if the positive equilibrium of (2.3) is asymptotically stable, and we aim to maximize the average population size, then the optimal harvesting strategy is $\theta = 0$, that is, harvesting at the beginning of the reproductive period. See Fig. 1.

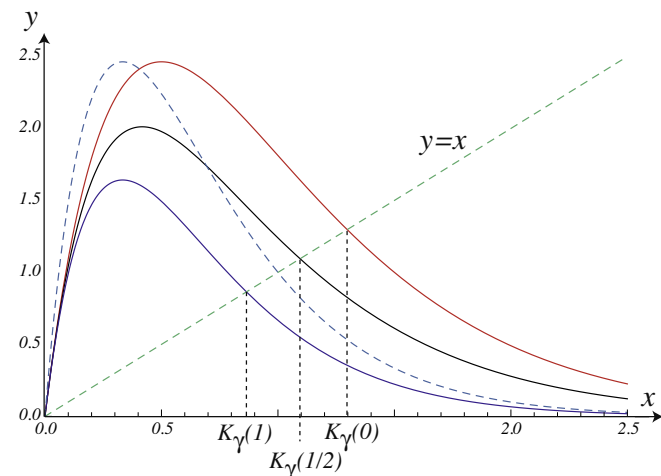


Fig. 1. Fixed points of $F_\theta(x)$ (equilibria of (2.3)) for different harvesting times $\theta = 0, 1/2, 1$ (solid lines from above to below), corresponding to harvesting early, in the middle and at the end of the season. The harvesting effort is $\gamma = 1/3$. The dashed curve is the (unharvested) Ricker map $f(x) = xe^{3(1-x)}$.

In the case of undercompensatory models such as the Beverton–Holt equation [39], the positive equilibrium is globally stable for $\gamma < \gamma^*$, and hence, according to Propositions 3.1 and 3.2, harvest timing only affects the population size.

In the remainder of this Section, we focus on overcompensatory models, which can exhibit unstable equilibria. We address the question how the harvesting effort γ and the harvesting time θ affect the stability properties of the positive equilibrium $K_\gamma(\theta)$ of (2.3). This study will give us a hint how to choose an appropriate harvesting time, in order to avoid some undesirable effects of harvesting.

As we have mentioned before, the maps F_0 and F_1 are topologically conjugated. One of the consequences is that the positive equilibrium $K_\gamma(0)$ of F_0 is asymptotically stable if and only if $K_\gamma(1)$ is asymptotically stable for F_1 (see [27]). However, for a general $\theta \in (0, 1)$ the map F_θ is not topologically conjugated to F_0 and F_1 . Even though we consider only two processes (harvesting and reproduction) [12–14], harvesting during the season (but neither right at the beginning nor at the end) induces different stability properties. This is because the harvest timing influences density-dependent effects. We now investigate this general case for some usual population models, distinguishing between uni- and bimodal maps.

3.1. Unimodal maps

We begin with the case of unimodal maps. If the positive equilibrium of (2.1) is unstable, then it is well known that increasing harvesting tends to stabilize the equilibrium after a series of period-halving bifurcations [40]. Actually, increasing harvesting cannot destabilize an asymptotically stable equilibrium of (2.1) (see, e.g., [27]).

We focus our attention on the Ricker map $f(x) = xe^{r(1-x)}$. In the absence of harvesting, the equilibrium $K = 1$ of (2.1) is asymptotically stable if and only if $r \leq 2$. Hence, if $r > 2$, the equilibrium is unstable, but harvesting in form of (2.3) can have a stabilizing effect. Figs. 2 and 3 in [19] suggest that the harvesting effort necessary for stabilization is less for values of $\theta \in (0, 1)$ than for $\theta = 0$ and $\theta = 1$. In the following, we prove that this claim is indeed true.

The next proposition was proved in [40]. As usual, we denote $F^2 := F \circ F, F^3 := F \circ F^2$ and so on.

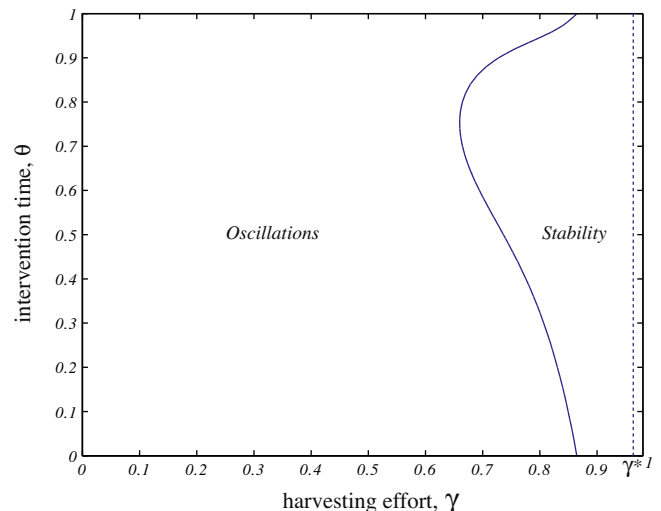


Fig. 2. Stability diagram for the positive equilibrium $K_\gamma(\theta)$ of (2.3) with $f(x) = xe^{4(1-x)}$ in the plane (γ, θ) . Note that intermediate harvest times $\theta \in (0, 1)$ can be stabilizing.

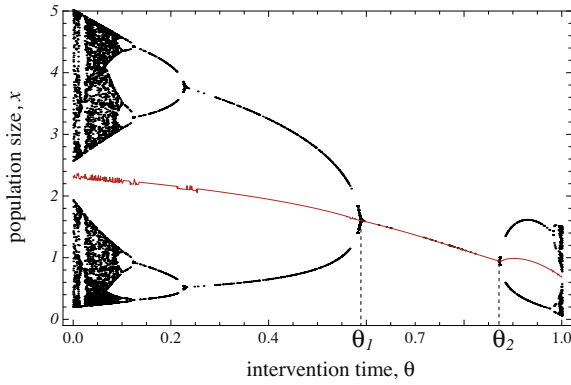


Fig. 3. Bifurcation diagram of population model (2.3) for varying harvesting times $\theta \in [0, 1]$. The thin red line represents the average population size after reproduction, which coincides with the equilibrium in the stable case. There are two flip bifurcation points at $\theta = \theta_1$ and $\theta = \theta_2$. The underlying population dynamics is the Ricker map $f(x) = xe^{4(1-x)}$ and the harvesting effort $\gamma = 0.7$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Proposition 3.3. Assume that $r > 2$. Then the positive equilibrium $K_\gamma(0)$ of (2.3) with $\theta = 0$ and $f(x) = xe^{r(1-x)}$ is asymptotically stable if and only if

$$\gamma_1 := 1 - e^{2-r} \leq \gamma < 1 - e^{-r} = \gamma^*. \tag{3.3}$$

Moreover, when (3.3) holds, $\lim_{n \rightarrow \infty} F_0^n(x) = K_\gamma(0)$ for all $x > 0$.

Of course, the conclusions of Proposition 3.3 also apply to $\theta = 1$. For a general $\theta \in (0, 1)$, however, it is difficult to get an explicit condition similar to (3.3). But we can prove that choosing a value of θ in the interior of $[0, 1]$ tends to be stabilizing, as Fig. 2 suggests.

Proposition 3.4. Assume that $r > 2$. Then the positive equilibrium $K_\gamma(\theta)$ of (2.3) with $\theta \in (0, 1)$ and $f(x) = xe^{r(1-x)}$ is asymptotically stable if condition (3.3) holds.

Proof. The statement of the proposition is proved if we show that $F'_\theta(K_\gamma(\theta)) > -1$ for all $\theta \in (0, 1)$ and $\gamma \in [\gamma_1, \gamma^*]$.

Elementary computations show that if $f(x) = xe^{r(1-x)}$ then the only critical point of f' is $P = 2/r$, and $f'(P)$ is a strict minimum of f' . In other words,

$$f'(x) > f'(P) \quad \text{for all } x > 0, \quad x \neq P. \tag{3.5}$$

Consider $\theta = 1$, and the map $F_1(x) = (1 - \gamma)f(x)$. The positive equilibrium $K_\gamma(1)$ becomes asymptotically stable at $\gamma = \gamma_1 = 1 - e^{2-r}$, for which $F'_1(K_{\gamma_1}(1)) = -1$.

Notice that for γ_1 the positive equilibrium $K_\gamma(1)$ is precisely $P = 2/r$. Indeed, if $x > 0$ and $\gamma = \gamma_1$, then

$$\begin{aligned} F_1(x) = x &\iff (1 - \gamma_1)e^{r(1-x)} = 1 \iff e^{2-r}e^{r(1-x)} = 1 \iff \\ e^{2-rx} = 1 &\iff x = \frac{2}{r} = P. \end{aligned}$$

Hence,

$$(1 - \gamma_1)f'(P) = F'_1(K_{\gamma_1}(1)) = -1. \tag{3.6}$$

We claim that

$$\begin{aligned} x \in (K_\gamma(1), K_\gamma(0)) &\implies \min\{F'_0(x), F'_1(x)\} > -1, \\ \forall \theta \in (0, 1) \text{ and } \gamma &\in [\gamma_1, \gamma^*]. \end{aligned}$$

By Proposition 3.2, and taking into account that F'_θ is a convex combination of F'_0 and F'_1 , this claim implies that (3.4) holds.

We now distinguish the cases $\gamma = \gamma_1$ and $\gamma > \gamma_1$.

(i) $\gamma > \gamma_1$. If $f'(x) > 0$ then $F'_1(x) = (1 - \gamma)f'(x) > 0$. If $f'(x) < 0$ then, since $\gamma > \gamma_1$, we get from (3.5) and (3.6) that

$$F'_1(x) = (1 - \gamma)f'(x) > (1 - \gamma_1)f'(x) \geq (1 - \gamma_1)f'(P) = -1.$$

Analogously, if $f'((1 - \gamma)x) > 0$ then $F'_0(x) = (1 - \gamma)f'((1 - \gamma)x) > 0$. If $f'((1 - \gamma)x) < 0$ then

$$\begin{aligned} F'_0(x) = (1 - \gamma)f'((1 - \gamma)x) &> (1 - \gamma_1)f'((1 - \gamma)x) \\ &\geq (1 - \gamma_1)f'(P) = -1. \end{aligned}$$

(ii) $\gamma = \gamma_1$. In this case, $K_{\gamma_1}(1) < x < K_{\gamma_1}(0)$ implies that $x \neq K_{\gamma_1}(1) = P$ and $(1 - \gamma_1)x \neq (1 - \gamma_1)K_{\gamma_1}(0) = K_{\gamma_1}(1) = P$. Therefore, $f'(x) > f'(P)$ and $f'((1 - \gamma_1)x) > f'(P)$. With this remark in mind, we have:

$$\begin{aligned} F'_1(x) &= (1 - \gamma_1)f'(x) > (1 - \gamma_1)f'(P) = -1; \\ F'_0(x) &= (1 - \gamma_1)f'((1 - \gamma_1)x) > (1 - \gamma_1)f'(P) = -1. \end{aligned} \quad \square$$

For other related population models (that are different from the Ricker map but still overcompensatory), our numerical simulations suggest that the following conjecture is true.

Conjecture 3.5. Assume that conditions (i)–(iii) in the statement of Proposition 3.1 hold, and that f is a unimodal map. If the positive equilibrium $K_\gamma(0)$ of (2.3) with $\theta = 0$ is asymptotically stable, then $K_\gamma(\theta)$ is asymptotically stable for (2.3) for all $\theta \in (0, 1)$.

For example, for the Maynard Smith (or generalized Beverton–Holt) map [41,42], defined by $f(x) = rx/(1 + x^\beta)$, $r > 1$, $\beta \geq 1$, it is easy to prove (see Appendix S1 in [26] and Theorem 1 in [40]) that the equilibrium $K_\gamma(0)$ is globally asymptotically stable if $\beta > 2$ and

$$1 - \frac{\beta}{r(\beta - 2)} \leq \gamma < 1 - \frac{1}{r}. \tag{3.7}$$

However, the same arguments used in the proof of Proposition 3.4 do not seem to work to prove an analogous result for (2.3) with $\theta \in (0, 1)$.

A special case is the quadratic map $f(x) = rx(1 - x)$, for which the positive equilibrium of (2.3) becomes asymptotically stable at the same critical harvest effort γ , regardless the value of $\theta \in [0, 1]$.

Indeed, the positive equilibrium

$$K_\gamma(\theta) = \frac{(1 - \gamma)r - 1}{(1 - \gamma)r(1 - \gamma + \gamma\theta)}$$

of (2.3) (with f being the quadratic map) is asymptotically stable if and only if $r(1 - \gamma) \leq 3$ (see also [19, p. 67]). This fact means that increasing harvesting stabilizes the positive equilibrium, and that the harvesting effort necessary to achieve this is independent of the value of θ , that is, of the harvesting time. Since a positive equilibrium only exists when $r(1 - \gamma) > 1$, we have the following result:

Proposition 3.6. Assume that $r > 3$. Then the positive equilibrium $K_\gamma(\theta)$ of (2.3) with $f(x) = rx(1 - x)$ is asymptotically stable for all values of $\theta \in [0, 1]$ if and only if

$$1 - \frac{3}{r} \leq \gamma < 1 - \frac{1}{r}. \tag{3.8}$$

Moreover, when (3.8) holds, all positive solutions of (2.3) converge to $K_\gamma(\theta)$.

The stabilization properties may be very helpful for management. For an example, we use the Ricker map $f(x) = xe^{4(1-x)}$. Assume that we plan to catch 70% from the stock (so $\gamma = 0.7$). For $\theta = 0$, Eq. (2.3) is chaotic, inducing a risk of extinction because the population floor is very low (see Fig. 3). If we want to prevent

the population to reach low densities, an optimal strategy is fixing the harvesting time at $\theta = \theta_1 \approx 0.5855$, where the equilibrium is stabilized at a value of $K_\gamma(\theta_1) \approx 1.609$, which after harvesting becomes $(1 - \gamma)K_\gamma(\theta_1) \approx 0.483$. If, on the contrary, we aim to control a plague in order to avoid bursts of high density, a good harvesting time is $\theta = \theta_2 \approx 0.873$, for which the equilibrium is still stable and takes a value $K_\gamma(\theta_2) \approx 0.943 < K_\gamma(\theta_1)$. For $\theta > \theta_2$, not only is the equilibrium destabilized (leading to higher population variability and thus to undesired high densities in some periods), but there is also a slight increase in the mean population size, following a flip bifurcation (see again Fig. 3).

3.2. Bimodal maps

In this section we deal with the case when f is a bimodal map in Eq. (2.3). We shall focus on the Clark–Ricker map

$$f(x) = \alpha x + (1 - \alpha)x e^{r(1-x)}, \tag{3.9}$$

where $\alpha \in (0, 1)$ stands for the survival of adults from one period to the next, and $r > 0$ is a growth parameter (see [43,27] for more details). Eq. (3.9) was suggested by Clark [22], and recently employed by Shelton and Mangel [44] to study how fishing can magnify fluctuations in fish populations, and by Yakubu et al. [23] to assess the performance of constant effort fishing. See also [43,35,27].

Before describing our results for the Clark–Ricker map we note that completely similar results are obtained for a modified Maynard Smith map with adult survivorship

$$f(x) = \alpha x + (1 - \alpha) \frac{rx}{1 + x^\beta}.$$

This map was used by Milton and Bélair [45] to describe the growth of bobwhite quail populations.

In the following we discuss the dynamics of Eq. (2.3) with f given by (3.9), that is,

$$x_{n+1} = \theta(1 - \gamma)(\alpha x_n + (1 - \alpha)x_n e^{r(1-x_n)}) + (1 - \theta)(1 - \gamma)(\alpha x_n + (1 - \alpha)x_n e^{r(1-(1-\gamma)x_n)}). \tag{3.10}$$

Theorem 2 in [27] states that, for $\theta = 0$, the positive equilibrium of (3.10) is destabilized as the harvesting effort γ is increased if and only if the other parameters α and r satisfy the following inequalities:

$$1 - \frac{2}{r} < \alpha < \frac{e^{r-3}}{2 + e^{r-3}}, \quad r > 3.$$

We choose $r = 4$ as a case study, in such a way that the equilibrium of (3.10) with $\theta = 0$ is destabilized by an increasing harvest-

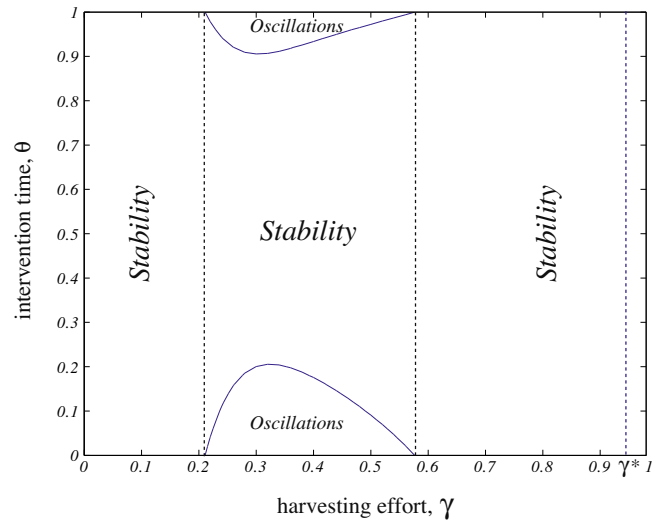


Fig. 5. Stability diagram of the bimodal map (3.10) for $r = 4$ and $\alpha = 0.55$.

ing if $\alpha \in (0.5, 0.576)$ (see [27] for more details). Actually, increasing harvesting leads to the emergence of *bubbles* (see [27, Definition 3]). This is illustrated in the bifurcation diagram of Fig. 4 (a) for $\theta = 0$. Harvesting at an intermediate moment of the season has the effect that the bubbles disappear; see Fig. 4 (a) for $\theta = 0.5$ (showing a stable equilibrium for all values of γ). Fig. 4 (b) shows the bifurcation diagram with the harvesting time θ as the bifurcation parameter. The stabilizing effect of intermediate harvesting times occurs in an interval (θ_1, θ_2) , with $\theta_1 \approx 0.175$ and $\theta_2 \approx 0.933$.

Fig. 5 shows a stability diagram of (3.10) in the plane of parameters (γ, θ) . While for values of θ either close to 0 or to 1 the equilibrium becomes unstable as γ is increased, this is not the case for intermediate values of θ , for which the equilibrium remains asymptotically stable (actually it seems to be globally stable).

For low adult survivorships, harvesting can magnify fluctuations in (3.10) with $\theta = 0$ in a more dramatic way, destabilizing a 2-periodic orbit to a chaotic attractor [27]. For example, for $\alpha = 0.02$, $\gamma = 0.65$ and $r = 4$, Eq. (3.10) with $\theta = 0$ is chaotic, with a very low population floor. The bifurcation diagram in Fig. 6 shows that for an appropriate harvesting timing, Eq. (3.10) has a 2-periodic attractor. Even though the mean population size is lower, this dynamical behavior reduces the chance of extinction due to

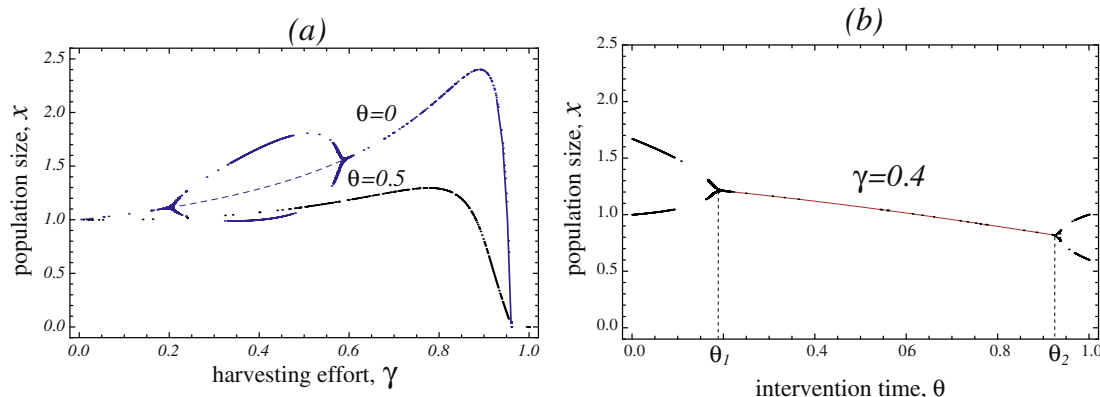


Fig. 4. Bifurcation diagrams of the bimodal map (3.10) with adult survival. (a) As γ is increased, a bubble is seen for $\theta = 0$. But for $\theta = 1/2$, the equilibrium seems to be globally stable for all values of γ . (b) For a fixed $\gamma = 0.4$, the equilibrium is stabilized at intermediate values of the harvesting time θ . Other parameter values: $r = 4$ and $\alpha = 0.55$.

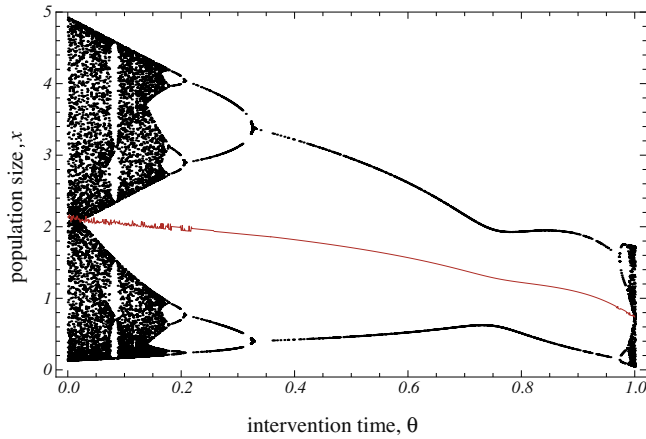


Fig. 6. Bifurcation diagram of the bimodal map (3.10) with a low adult survivorship $\alpha = 0.02$. Note that later harvesting (increasing θ) increases the population floor, i.e. the minimum population size, and also stabilizes the dynamics over a large parameter range. The mean population size (thin red line) is reduced. Other parameter values: $\gamma = 0.65$ and $r = 4$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

stochastic perturbations, since the minimum population sizes have increased.

4. Models with Allee effect

In this section, we explore the influence of the harvesting time parameter θ in Eq. (2.3) when f describes the growth of a population which exhibits a strong Allee effect [46]. The Allee effect describes positive density-dependence at small population sizes (e.g., due to cooperation). At larger population sizes, negative density-dependence prevails (e.g., due to resource competition), and the dynamics can be under- or overcompensatory. We will consider both cases.

4.1. Modified Beverton–Holt model

We begin with a modified Beverton–Holt model

$$x_{n+1} = \frac{\alpha x_n^2}{1 + \beta x_n^2}, \tag{4.1}$$

where α and β are positive constants. This equation has been proposed by Hoppensteadt [47], and more recently used in [48,23]; see also [49,50]. It is an example for undercompensatory population dynamics with strong Allee effect.

The function

$$f(x) = \frac{\alpha x^2}{1 + \beta x^2} \tag{4.2}$$

is differentiable and increasing in $(0, \infty)$. If $\alpha^2 > 4\beta$, then f has exactly two positive fixed points $K_1 < K_2$. The smaller one is unstable, as $f'(K_1) > 1$, and the larger one is asymptotically stable, as $f'(K_2) < 1$. K_1 is the so-called Allee threshold: solutions of (4.1) converge to zero for initial conditions $x_0 < K_1$ or to the carrying capacity K_2 for initial conditions $x_0 > K_1$.

An important difference to the compensatory models studied in Section 3 is that overharvesting populations with Allee effect leads to extinction via a saddle–node bifurcation [51,23]. For $\theta = 0$ and $\theta = 1$, it is easy to prove (see [23] and Proposition 4.1 below) that there is a critical value γ_0^* of the harvesting effort such that a population governed by (2.3) and (4.2) exhibits bistability if $\gamma < \gamma_0^*$, and extinction occurs if $\gamma > \gamma_0^*$. For $\gamma < \gamma_0^*$, there are three equilibria $0 < K_1(\gamma, \theta) < K_2(\gamma, \theta)$, with 0 and K_2 being asymptotically stable

and K_1 being unstable. For $\gamma = \gamma_0^*$, the two positive equilibria coincide: $K_1(\gamma_0^*, \theta) = K_2(\gamma_0^*, \theta) := K_0^*$, and $F_\theta(K_0^*) = 1$.

For $\theta \in (0, 1)$, since F_θ is increasing and a convex combination of F_0 and F_1 , it follows by continuity that there is a corresponding critical value γ_0^* such that extinction occurs if $\gamma > \gamma_0^*$. In contrast to Proposition 3.1, this critical value does depend on the harvesting time θ . This is a novel result. Actually, the critical harvesting effort attains its maximum value for $\theta = 0$ and $\theta = 1$, as the following result shows.

Proposition 4.1. Let us consider Eq. (2.3) with f given by (4.2). Then:

- (a) The critical value of the harvesting time for a saddle–node bifurcation to occur with $\theta = 0$ and $\theta = 1$ is

$$\gamma_1^* = \gamma_0^* = 1 - \frac{2\sqrt{\beta}}{\alpha}.$$

- (b) If $\theta \in (0, 1)$ and $\gamma \geq \gamma_1^*$, then $F_\theta(x) < x$ for all $x > 0$. Thus, $\gamma_0^* < \gamma_1^* = \gamma_0^*$, for all $\theta \in (0, 1)$.

Proof. The value of γ_0^* is immediately obtained from the equation $K_1(\gamma, 0) = K_2(\gamma, 0)$, which is equivalent to $4\beta = (\alpha - \alpha\gamma)^2$. The value of γ_1^* is also easily obtained; both values are equal because $F_0(x) = f((1 - \gamma)x)$ and $F_1(x) = (1 - \gamma)f(x)$ are topologically conjugated.

To prove statement (b) of the proposition, notice that for $\gamma = \gamma_1^*$ the only positive equilibrium of F_1 is $K_1^* = 1/\sqrt{\beta}$, and the only positive equilibrium of F_0 is $K_0^* = f(K_1^*) = \alpha/(2\beta)$. Moreover, $K_0^* \neq K_1^*$ because $\alpha^2 > 4\beta$.

On the other hand, $F_i(x) < x$ for all $x > 0$, $x \neq K_i^*$, $i = 0, 1$. Since $F_\theta(x)$ is a convex combination of $F_0(x)$ and $F_1(x)$, it follows that $F_\theta(x) < x$ for all $x > 0$ and all $\theta \in (0, 1)$. Thus, claim (b) is true for $\gamma = \gamma_1^*$. If $\gamma > \gamma_1^*$, then both $F_1(x)$ and $F_0(x)$ are less than x for all $x > 0$, and therefore the same convexity argument applies to conclude that $F_\theta(x) < x$ for all $x > 0$. \square

Proposition 4.1 implies that harvesting at an intermediate moment θ in the season makes the population more prone to extinction. This is illustrated in Fig. 7, which summarizes the dynamical outcomes in the parameter plane (γ, θ) .

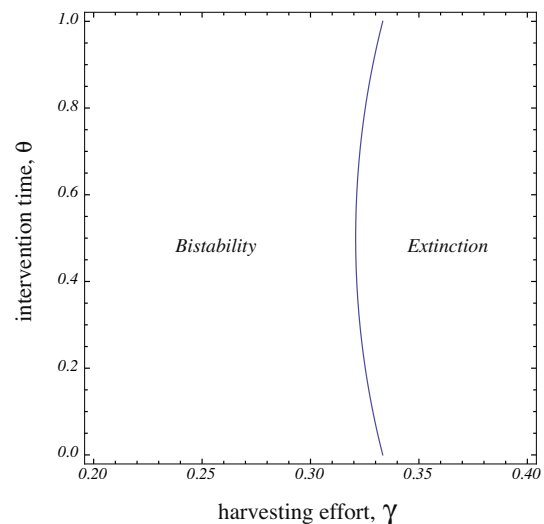


Fig. 7. Survival/extinction diagram for the Allee effect model (2.3), (4.1) with a modified Beverton–Holt map $f(x) = 3x^2/(1 + x^2)$ in the plane (γ, θ) . Note that the bistability regime allows survival (or extinction) for sufficiently large (or small, respectively) initial population sizes.

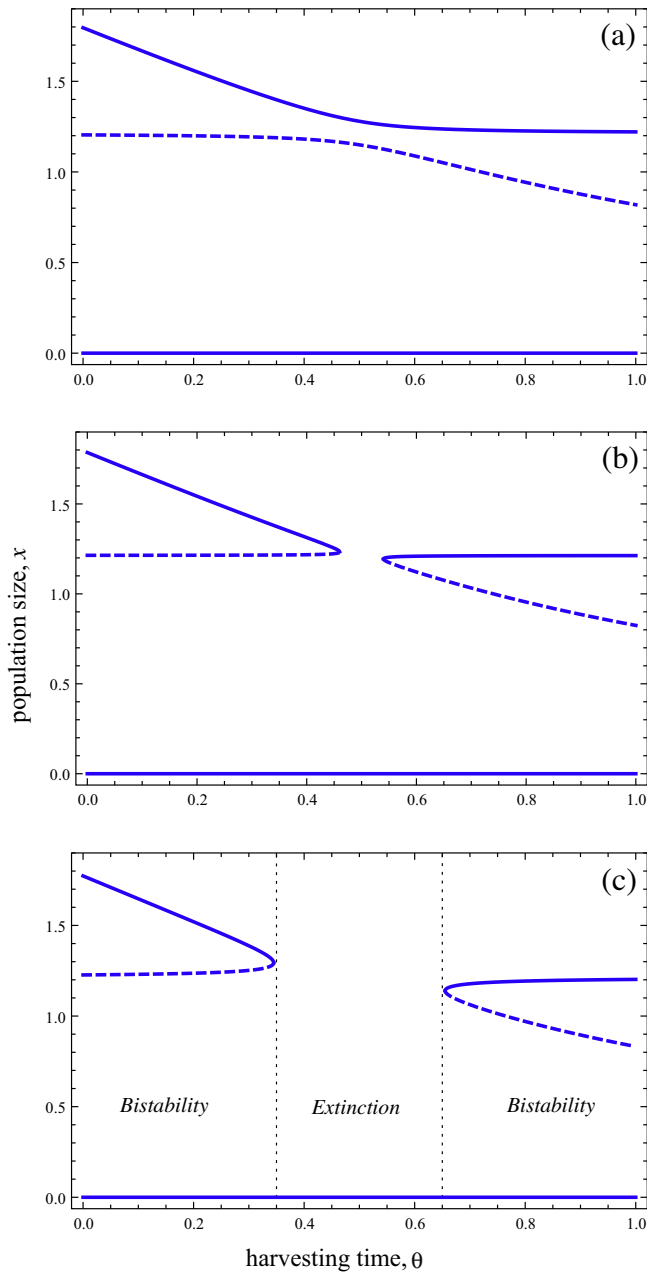


Fig. 8. Bifurcation diagrams of the Allee effect model (2.3), (4.1) with a modified Beverton–Holt map $f(x) = 3x^2/(1+x^2)$ for increasing harvesting efforts: (a) $\gamma = 0.32$, (b) $\gamma = 0.3209$ and (c) $\gamma = 0.322$; using the intervention time θ as the bifurcation parameter.

Fig. 8 reveals why intermediate harvesting times can induce extinction. For low harvesting (Fig. 8a), both the carrying capacity K_2 and the Allee threshold K_1 decline with later harvesting times. However, they do so with different rates. The carrying capacity decreases quickly for early harvesting, but becomes less affected by later harvesting, whereas the effect on the Allee threshold is vice versa. In consequence, if we increase the harvesting moment θ , the carrying capacity and Allee threshold approach each other. If we then increase the harvesting effort (Fig. 8b), the two equilibria collide and annihilate each other. This results in a parameter range of extinction for intermediate harvesting times, while the population dynamics is still bistable for harvesting times early or late in the season (Fig. 8c). Note that the population size at the (asymptotically stable) carrying capacity increases with θ for late harvesting

times, which is in contrast to all previous observations (cf. Proposition 3.2 for compensatory maps without Allee effect).

4.2. Modified Ricker model

We now consider a population model with overcompensation and Allee effect, namely,

$$x_{n+1} = \frac{\alpha x_n^2}{1 + \alpha x_n} e^{r(1-x_n)}, \tag{4.3}$$

where α and r are positive constants. Eq. (4.3) is a Ricker model modified with a positive density factor $I(x) = \alpha x/(1 + \alpha x)$, and it has been used by Schreiber [51] to model mate limitation. The parameter α represents the carrying capacity of the population in the absence of mate limitation multiplied by an individual's efficiency to find a mate [51, Section 2.1].

In this model, transition to extinction due to overharvesting also takes place via a saddle–node bifurcation; cf. Fig. 9. This is similar to the modified Beverton–Holt map considered before and a consequence of the strong Allee effect. There are two differences, however, which can be related to the overcompensatory dynamics of the modified Ricker map. Firstly, bistability does not necessarily mean that two asymptotically stable equilibria coexist. In general, the extinction equilibrium $x = 0$ coexists with a nontrivial attractor whose dynamics ranges between an asymptotically stable equilibrium and what seems to be a chaotic attractor (cf. Fig. 9 at intermediate harvesting efforts).

Secondly, the complex dynamics of the nontrivial attractor can interplay with the Allee threshold. This gives rise to the phenomenon of essential extinction, which can occur for certain values of α and r . The map $f : [0, \infty) \rightarrow [0, \infty)$ defined by

$$f(x) = \frac{\alpha x^2}{1 + \alpha x} e^{r(1-x)} \tag{4.4}$$

has a unique critical point $c > 0$, which is a global maximum of f . Essential extinction occurs when f has two positive fixed points $K_1 < K_2$, and $f(c) < K_1$. In this situation, for a randomly chosen initial condition, extinction occurs with probability one; however, the set of initial conditions that do not lead to extinction is nonempty, and define a chaotic repeller [51].

Thus, for the dynamics of model (4.3), there are three generic possibilities: (monostable) extinction due to overharvesting; bistability between extinction and (possibly complex) survival; and essential extinction. The transition from essential extinction to bistability takes place via a boundary collision [43,52]. The transition from bistability to extinction occurs, as in (4.1), via a saddle–node bifurcation.

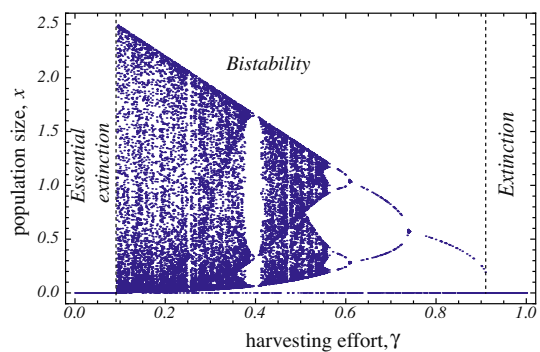


Fig. 9. Bifurcation diagram of the Allee effect model (2.3), (4.3) with an overcompensatory Ricker map $f(x) = e^{d(1-x)}4x^2/(1+4x)$ and $\theta = 1$, using the harvesting effort γ as the bifurcation parameter.

We study the influence of the harvesting time parameter θ on the dynamics of (2.3) when f is defined by (4.4). Our first observation is that the same arguments used in the proof of Proposition 4.1 apply to demonstrate that intermediate values of θ make the population more prone to extinction by overharvesting.

Next, our numerical simulations show that, as it occurs for the overcompensatory models studied in Section 3, harvesting at an intermediate value of θ can stabilize the population dynamics (in terms of simplifying them).

Finally, regarding the transition between bistability and essential extinction, we observe that the population can survive if harvesting occurs at an intermediate moment of the reproductive season under the same harvesting strength for which there is essential extinction for $\theta = 0$ and $\theta = 1$.

As a case study, we choose $\alpha = 4$ and $r = 4$. For these values, essential extinction is observed in model (4.3) (c.f. [51, p. 205]). When constant effort harvesting is applied for $\theta = 0$ or $\theta = 1$ in (2.3) with this function f , a catastrophe bifurcation switches the dynamics from essential extinction to bistability at a value $\gamma_1 = 0.09384$. A tangent bifurcation leads to extinction at $\gamma_2 = 0.91104$. Between γ_1 and γ_2 , the dynamics of the nontrivial attractor ranges from chaos to asymptotic stability of the greatest positive equilibrium. See Fig. 9.

We now fix three different values of the harvesting effort γ to illustrate the changes in the dynamics when the harvesting time θ is the bifurcation parameter.

- For low harvesting ($\gamma = 0.09$), intermediate values of θ prevent essential extinction (see Fig. 10).
- For intermediate harvesting ($\gamma = 0.58$), intermediate values of θ are stabilizing (see Fig. 11).
- For high harvesting ($\gamma = 0.88$), intermediate values of θ can lead to extinction (not shown here, because the diagram is similar to Fig. 8).

The full diagram for $\theta \in [0, 1]$ and $\gamma \in [0, 1]$ is shown in Fig. 12.

5. Discussion

This paper shows that the timing of harvesting can profoundly change the impact of the exploitation on the population. We have not only considered the population size (which determines the yield), but we have focused particularly on the stability properties. They drive the inherent population variability and are important factors in the context of extinction and outbreaks.

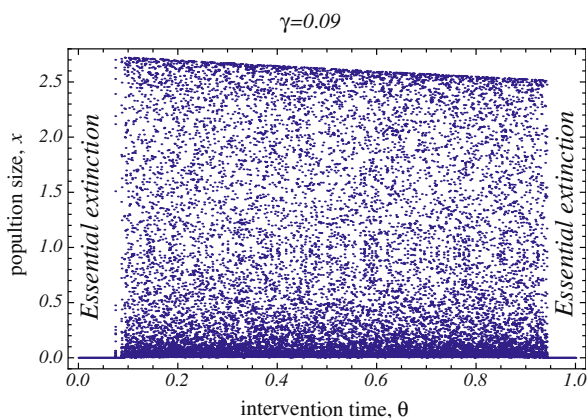


Fig. 10. Bifurcation diagram of the Allee effect model (2.3), (4.3) with an overcompensatory Ricker map $f(x) = e^{4(1-x)}4x^2/(1+4x)$ and $\gamma = 0.09$, using the intervention time θ as the bifurcation parameter. Essential extinction for values of θ close to 0 and 1 and bistability for intermediate values.

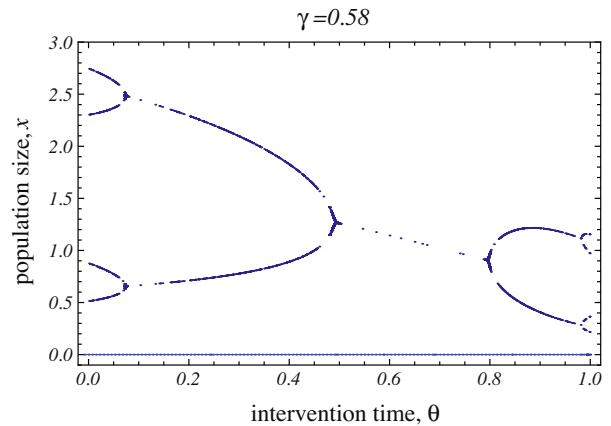


Fig. 11. Bifurcation diagram of the Allee effect model (2.3), (4.3) with an overcompensatory Ricker map $f(x) = e^{4(1-x)}4x^2/(1+4x)$ and $\gamma = 0.58$, using the intervention time θ as the bifurcation parameter. Stabilization of the carrying capacity for intermediate values of θ .

For overcompensatory population dynamics (without Allee effect), the models investigated predict that a harvest timing in the mid-season has a stabilizing effect on the population. This holds for both uni- and bimodal maps (like the Ricker and Clark–Ricker map, respectively). For unimodal maps, harvesting generally tends to be stabilizing [30,31], and this effect can be further enhanced by a proper timing. For bimodal maps, harvesting can induce bubbling and thus be both destabilizing (for intermediate harvesting efforts) as well as stabilizing (for larger harvesting efforts). Here, harvesting mid-season can prevent the bubbles to appear and therefore again promotes the stabilizing impact of harvesting.

There are only few previous theoretical studies that explored the consequences of different harvest timing, and even fewer take into account the population stability. Jonzen and Lundberg observe that “harvesting, no matter when, stabilizes the dynamics” [13, p. 41], but they consider harvest timing only in different order relative to birth and death events. Tang and Chen [17] show that later harvest timings are stabilizing, whereas Xu et al. [18] find that early harvest timings are more stabilizing than others.

The results in this paper contradict both of these earlier findings. It should be noted, however, that the models are somewhat difficult to compare. Both Refs. [17,18] assume a non-impulsive continuous period of harvesting that stretches over certain times of the season, with the former considering stage structure and the latter considering periodic environmental fluctuations.

This paper employs the harvesting model proposed by Seno [19]. While it is probably one of the simplest models to account for variable harvest timings, it makes a number of simplifying assumptions and, to our knowledge, currently appears to lack a mechanistic derivation.

Regarding population size, previous models [7,17,18] find that later harvesting times reduce equilibrium population size (and thus the achievable yield), because late harvesting cuts into breeding stock of the next generation and may not take advantage of compensatory population growth effects. The results for the Seno model (see Proposition 3.2) are in line with this theory—provided there is no Allee effect (see our Discussion below). Moreover, we find that the critical harvesting effort that leads to extinction is independent of the harvest timing. Hence, overexploitation due to too large harvesting effort cannot be prevented by a different choice of timing. However, this also changes when we account for the Allee effect.

To our knowledge, Allee effects have been completely ignored in studies of harvest timing. Here, we find that the presence of a strong Allee effect can dramatically alter the impact of different

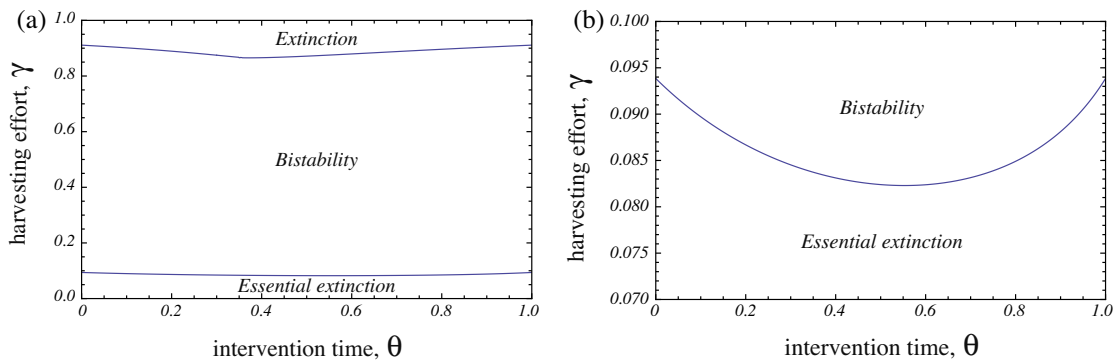


Fig. 12. Survival/extinction diagrams of the Allee effect model (2.3), (4.3) with an overcompensatory Ricker map $f(x) = e^{4(1-x)}4x^2/(1+4x)$, in the plane (θ, γ) . (a) The three different generic categories for $\theta \in [0, 1]$ and $\gamma \in [0, 1]$. (b) The boundary between essential extinction and bistability for $\theta \in [0, 1]$ and $\gamma \in [0.07, 0.1]$, to emphasize how essential extinction can be prevented for intermediate values of θ .

Table 1
Summary of results

	without Allee effect	with strong Allee effect
Compensatory models	Critical effort leading to overharvesting independent of harvest timing (Prop. 3.1) Population size decreases monotonically with harvest timing (Prop. 3.2)	Critical harvesting effort does depend on harvest timing (Prop. 4.1): Intermediate harvest timing makes the population more prone to extinction Population size may increase with later harvesting (Fig. 8c)
Overcompensation (unimodal maps)	Intermediate harvesting times are stabilizing (Prop. 3.4)	Intermediate harvesting times can be stabilizing (Fig. 11) Intermediate harvesting times can promote survival if the harvesting effort is small (Fig. 10) Intermediate harvesting times can induce extinction if the harvesting effort is large (Fig. 12, Prop. 4.1)
Overcompensation (bimodal maps)	Intermediate harvesting times are stabilizing, i.e. 'bubbles' disappear (Sect. 3.2)	Not considered

harvest times (see the summary of results in Table 1). First of all, as already mentioned, the critical harvesting effort leading to overexploitation does depend on θ (see Proposition 4.1). To be more precise, harvesting mid-season rather than early or late in the season renders the population more vulnerable. This turns the previous results from overcompensatory models upside down, where intermediate harvest times are stabilizing (and may thus enhance persistence). In the presence of a strong Allee effect, by contrast, intermediate harvest times promote overexploitation.

Second, the relationship between population size at stable equilibrium and harvest timing is no longer monotonic. As discussed before, this used to be a key result and one of the common grounds in the literature. A strong Allee effect, however, may induce an increase in population size with later harvest timing (see Fig. 8c). We have found this to occur for high harvesting efforts and when harvesting takes place late in the season. This effect can be observed in Allee effect models with both under- and overcompensation (e.g., the modified Beverton–Holt and the modified Ricker maps, respectively).

Third, when populations with Allee effect and overcompensation are doomed to essential extinction for harvesting regimes early or late in the season, intermediate harvest timing can facilitate their survival (see Fig. 10). We have also shown that intermediate harvest timing can be stabilizing (see Fig. 11). Hence, Allee effects can enhance both persistence as well as extinction when harvesting mid-season; the actual outcome may depend on the magnitude of the harvesting effort (see Section 4.2).

In the presence of a strong Allee effect, harvest timing impacts not only on the population size at carrying capacity, but also on the Allee threshold—which in turn determines the critical population size for extinction. Harvesting early leaves the population little time to grow above the Allee threshold. Therefore, it may be better to harvest later in the season when the population has grown large

enough in size. However, there is clearly a trade-off, because later harvesting also tends to reduce the population size. Depending on which one of the two positive equilibria (Allee threshold and carrying capacity) decreases more quickly with later harvesting, this may induce extinction or facilitate survival.

Some of the results in this paper are based on numerical simulations, especially those regarding the Allee effect. They are therefore not as rigorous as the analytical results. Nevertheless, by exploring a relatively wide range of parameter values, we have captured emerging trends how harvest timing affects population dynamics, stability and persistence.

This paper suggests that not only the harvesting effort, but also its timing are crucial in designing management programmes of exploited populations. For the same effort of harvesting, choosing a different moment in time can drastically alter the population-level consequences. In particular, the Seno model suggests that intermediate harvesting times tend to be stabilizing, but that the presence of Allee effects may turn the consequences of harvesting upside-down.

Acknowledgements

E. Liz was supported in part by the Spanish Government and FEDER, grant MTM2010–14837. F.M. Hilker acknowledges support from a Santander research travel grant. The authors wish to thank the referees for their comments.

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