Adaptive threshold harvesting and the suppression of transients

Juan Segura [a], Frank M. Hilker [b], Daniel Franco [a,*]

[a] Departamento de Matemática Aplicada, E.T.S.I. Industriales, Universidad Nacional de Educación a Distancia (UNED), c/ Juan del Rosal 12, 28040, Madrid, Spain
[b] Institute of Environmental Systems Research, School of Mathematics/Computer Science, Osnabrück University, Barbarastr. 12, 49076 Osnabrück, Germany

HIGHLIGHTS

- We present an adaptive harvesting strategy to reduce population fluctuations.
- The strategy is useful for exploited species or to prevent outbreaks.
- It provides an alternative to *adaptive limiter control*.
- Transient dynamics can profoundly raise the short-term yield.
- We propose adjusted control strategies that reduce the length of transients.

ARTICLE INFO

ABSTRACT

Fluctuations in population size are in many cases undesirable, as they can induce outbreaks and extinctions or impede the optimal management of populations. We propose the strategy of adaptive threshold harvesting (ATH) to control fluctuations in population size. In this strategy, the population is harvested whenever population size has grown beyond a certain proportion in comparison to the previous generation. Taking such population increases into account, ATH intervenes also at smaller population sizes than the strategy of threshold harvesting. Moreover, ATH is the harvesting version of adaptive limiter control (ALC) that has recently been shown to stabilize population oscillations in both experiments and theoretical studies. We find that ATH has similar stabilization properties as ALC and thus offers itself as a harvesting alternative for the control of pests, exploitation of biological resources, or when restocking interventions required from ALC are unfeasible. We present numerical simulations of ATH to illustrate its performance in the presence of noise, lattice effect, and Allee effect. In addition, we propose an adjustment to both ATH and ALC that restricts interventions when control seems unnecessary, i.e. when population size is too small or too large, respectively. This adjustment cancels prolonged transients.

1. Introduction

Due to their recurring and sometimes unpredictable ups and downs, fluctuations in population size pose several challenges for biological conservation and the management of wildlife and exploited populations. Intervention strategies have been developed to reduce the outbreak frequency and extinction probability (Hilker and Westerhoff, 2007a), stabilize the fluctuations (Hudson et al., 1998; Korpimäki and Norrdahl, 1998; Desharnais et al., 2001), and maximize the yield of harvested populations (Lande et al., 1995; Hudson and Dobson, 2001).

Here, we propose and analyze a harvesting strategy that takes effect only if the population size has grown by at least a certain factor in comparison to the previous census. This conditional strategy differs from textbook strategies like constant-effort and constant-yield harvesting, as it responds only to population increases sufficiently large. We shall refer to this strategy as *adaptive threshold harvesting* (*ATH*) and the *harvesting version of adaptive limiter control* (*h-ALC*), because it is closely related to threshold harvesting, also known as limiter control (LC), on the one hand and to adaptive limiter control (ALC) on the other hand.

Threshold harvesting removes individuals from a population whenever population size exceeds a fixed threshold value (Lande et al., 1997; Fryxell et al., 2005). This harvest control rule is equivalent to limiter control, which is a method originating from

* Corresponding author.
E-mail address: dfranco@ind.uned.es (D. Franco).

physics (Sinha, 1994; Corron et al., 2000; Wagner and Stoop, 2001) and has been applied to problems as diverse as computer architecture design (Ditto and Sinha, 2015), cardiac rhythms (Glass and Zeng, 1994), commodity markets (He and Westerhoff, 2005), and population dynamics (Hilker and Westerhoff, 2005, 2006). Limiter control methods have the advantage that no detailed information of the system is required, which is why they are easy and fast to implement. Similar to some other population control methods (e.g. McCallum, 1992; Parthasarathy and Sinha, 1995; Solé et al., 1999; Liz, 2010; Dattani et al., 2011; Franco and Perán, 2013; Tung et al., 2014), they directly affect the state variables, i.e. the population size, by restocking (adding) or harvesting (removing) individuals. This approach seems particularly apt for ecological systems that are characterized by intrinsic uncertainty and 'inaccessibility' of parameters such as life-history traits.

Adaptive limiter control has been recently proposed by Sah et al. (2013). The idea of ALC is to add individuals to the population whenever the population size falls below a certain fraction of its value in the previous generation. The term 'adaptive' follows from the fact that the threshold value of the population size triggering control is a fraction of the previous population size, and as such variable over time. The efficacy of ALC to stabilize biological populations has been shown in laboratory experiments on populations and metapopulations of the fruit fly *Drosophila melanogaster* (Sah et al., 2013) as well as by analytical results (Franco and Hilker, 2013) and numerical simulations (Sah et al., 2013; Franco and Hilker, 2013; Tung et al., 2014; Sah and Dey, 2014). ALC is therefore one of the few well-studied control strategies in ecology.

As a restocking strategy, ALC is likely to be applied in the context of conservation and re-introduction programs. Depending on the management objective and the ecological objective, however, there is clearly a need for an alternative based on harvesting. For instance, management programs directed to the control of pest species and species of commercial value (e.g., fisheries) aim to remove individuals from the population. Obviously, ATH appears relevant in the context of controlling outbreaks of nuisance species and exploiting biological resources.

Moreover, independent of any management objectives, there may be logistical restrictions of restocking strategies. They require the availability of a versatile source of individuals for supplementing the population if needed. However, such a pool of individuals may be difficult or even impossible to create or to maintain in practice. For instance, some organisms cannot be kept in captivity or do not reproduce in such conditions. Furthermore, there may be issues related to translocation and releasing individuals. Maintaining and managing a stock may be costly, labor-intensive, logistically challenging, and time-consuming. By contrast, removing individuals is certainly 'easier' than restocking in some situations. It should be noted, though, that removal methods may be difficult to implement as well and may raise ethical concerns about killing animals.

Being based on harvesting rather than restocking, the harvest control strategy presented in this paper is the harvesting version of adaptive limiter control. That is, whenever the population size exceeds a limit that is a certain proportion of the population size in the preceding generation, harvesting takes place and reduces the population size to that limit. In contrast to threshold harvesting, the critical population size above which interventions take place is not fixed, but is adaptive in response to the previous population size.

While the kind of control (restocking vs. harvesting) is motivated by the biological application, replacing restocking by harvesting may appear straightforward from a mathematical point of view. However, there is no reason to believe that the dynamical behavior induced by ALC on the one hand and by its harvesting version ATH on the other hand is similar. This becomes clear when considering other control strategies that have harvesting and

restocking variants. For instance, proportional feedback control (Güémez and Matías, 1993) is able to stabilize a population towards a positive equilibrium when a constant proportion of the population is harvested (Liz, 2010), but the restocking variant adding a constant proportion of the population fails to stabilize the equilibrium (Carmona and Franco, 2006). Constant feedback control provides another dramatic example. While adding or removing a constant number of individuals each generation can stabilize chaotic dynamics (McCallum, 1992; Gueron, 1998; Stone and Hart, 1999), the latter form of intervention can drive the population extinct at small removal rates, even when the population is able to persist for higher removal rates (Sinha and Parthasarathy, 1996; Schreiber, 2001). These examples arise in the simplest case of single-species models given by unimodal maps that we also consider in this paper.

In the next section, we introduce the mathematical model describing adaptive threshold harvesting. We then analyze its effect on the constancy stability in terms of two different measures, namely the fluctuation range and the fluctuation index. Mathematical proofs of the results presented in this section can be found in the Appendix. Since ATH is a harvesting strategy and the individuals removed may be actually of economic interest (e.g. in fisheries), Section 4 considers the mean yield per generation, both in the long-run and the short-run. Section 5 focuses on the short-term dynamics generated by the interventions. Transients are often ignored in theoretical studies of ecological systems, which is why we discuss in some detail how to deal with them. In particular, we propose adjusted versions of both ATH and ALC that reduce the length of transients and thus accelerate the approach to the long-term dynamics. Section 6 explores the robustness of ATH against noise, lattice effect, and Allee effect.

2. Adaptive threshold harvesting

2.1. Population growth model

The effect of a control method on a biological population depends on the underlying population dynamics, so we start by describing the model of the uncontrolled system. We assume that the population dynamics is described by a first-order one-dimensional difference equation

$$x_{t+1} = f(x_t), \quad x_0 \in [0, \infty), t \in \mathbb{N}, \tag{1}$$

where x_t denotes the population size at time step t. The population production map f is assumed to satisfy the following conditions:

(C1) $f : [0, b] \rightarrow [0, b]$ ($b = \infty$ is allowed) is continuously differentiable and such that $f(0) = 0$, $f(x) > 0$ for all $x \in (0, b)$ and $f'(0^+), f'(b^-) \in \mathbb{R}$.

(C2) f has two non-negative fixed points $x = 0$ and $x = K > 0$, with $f(x) > x$ for $0 < x < K$ and $f(x) < x$ for $x > K$.

(C3) f has a unique critical point $d \in (0, K)$ in such a way that $f(d) \leq b$, $f'(x) > 0$ for all $x \in (0, d)$ and $f'(x) < 0$ for all $x \in (d, b)$.

These conditions describe a unimodal population production function peaking at $x = d$ and are standard assumptions in the study of discrete-time population dynamics (e.g. May, 1976; Singer, 1978; Cull, 1981; Schreiber, 2001; Carmona and Franco, 2006; Franco and Hilker, 2013). Biologically speaking, the population has two fixed points, namely (i) the extinction state $x = 0$ and (ii) a positive equilibrium $x = K$, which corresponds to the carrying capacity of the population. Initial population sizes are smaller than b, and the dynamics are overcompensatory with no demographic Allee effect. Examples include the frequently considered population dynamics models in their overcompensatory regimes,
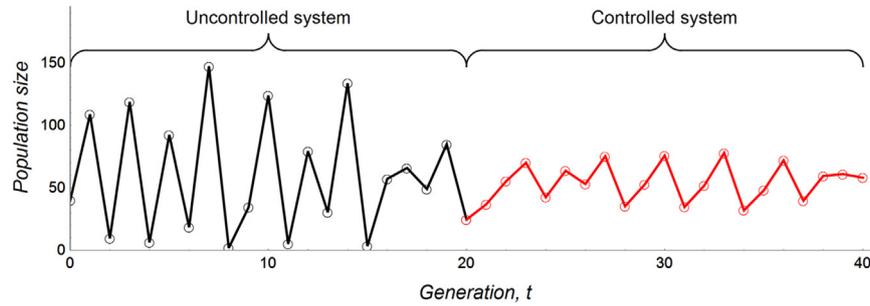
Fig. 1. During the first 20 generations, the population is uncontrolled and follows Eq. (1) for the Ricker map $f(x) = x\exp(r(1-x/K))$ with growth parameter $r=3$ and carrying capacity $K=60$. In the next 20 generations, the population is controlled by adaptive threshold harvesting with intensity $c=2/3$.

e.g. the Ricker (1954), Hassell (1975), and generalized Beverton–Holt (Bellows, 1981) maps.

2.2. Modelling adaptive threshold harvesting

Adaptive threshold harvesting exerts control on a population when the population size x_t at time step t exceeds a certain proportion of its value in the preceding generation. The control then restores the population size back to that threshold by harvesting the surplus individuals. Thus, ATH takes action if the population has grown beyond a certain proportion within a time step, which is why ATH can be seen as aiming to prevent population booms.

As ALC, this new limiter method is "adaptive" because the magnitude of the intervention is nonconstant and depends on the system state at the previous time step. Fig. 1 shows how ATH modifies the dynamics of the population and, in particular, how the fluctuation range of the population size is reduced.

When applying ATH, there are two different population sizes at time step t, namely b_t, the population size before ATH intervention and a_t, the population size after intervention. In particular, $b_t \geq a_t$ because ATH never adds individuals to the population. With these notations, the dynamics of ATH is determined by the following system of difference equations:

$$b_{t+1} = f(a_t) \quad \text{and} \quad a_{t+1} = \begin{cases} b_{t+1}, & b_{t+1} \leq a_t/c, \\ a_t/c, & b_{t+1} > a_t/c, \end{cases} \tag{2}$$

where $c \in (0,1)$ is a control parameter measuring the ATH intensity. Substituting the value for b_{t+1} from the first equation of system (2) into the second one, we obtain that the population dynamics is determined by the first-order difference equation

$$a_{t+1} = \begin{cases} f(a_t), & f(a_t) \leq a_t/c, \\ a_t/c, & f(a_t) > a_t/c, \end{cases} \tag{3}$$

which is piecewise smooth and can be written in one line by using the minimum function,

$$a_{t+1} = \min\{f(a_t), a_t/c\}.$$

2.3. Activation threshold

By definition, ATH only takes effect when the population size exceeds a proportion of its magnitude in the preceding generation. Any management implementing control must therefore wait until measuring the population size in generation t to decide about the need for intervention. Fortunately, the analysis of (3) reveals the existence of a 'hidden' threshold level A_T such that no control will be necessary in generation t if the population size in the preceding generation is above this value.

Such knowledge can be of practical interest because no preparation will need to be taken in this situation. Note that the
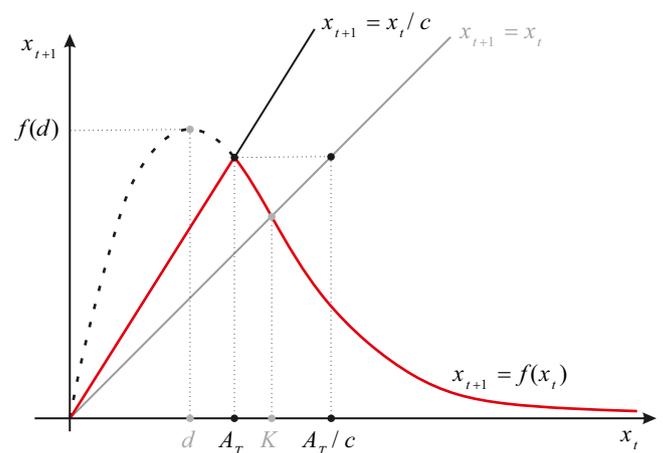
Fig. 2. Adaptive threshold harvesting only takes place when the straight line $a_{t+1} = a_t/c$ is under the graph of the population production map f. The activation threshold A_T is defined by their intersection. The bold red curve represents the population production function (3) for the controlled system. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

activation threshold for ALC has a different meaning, namely that control actions only take place if the activation threshold is exceeded in the preceding time step. In order to calculate the activation threshold for a given control parameter, we need to know the population production function which can be obtained from fitting to time series data. Proposition 1 in the Appendix shows the existence of A_T for control intensities $c > \inf_{x \in (0,b)} x/f(x)$ and its precise definition.

Although the determination of A_T in practical situations can be difficult due to noise or lack of information about the system variables, in deterministic systems its knowledge helps the controller to know early on when an intervention is unnecessary in the next generation.

3. Stabilization of fluctuations

Here we describe how adaptive threshold harvesting affects constancy stability, i.e. the propensity of the population size to stay essentially unchanged (Grimm and Wissel, 1997). First of all, ATH is not able to stabilize oscillations towards an equilibrium point (see Proposition 2 in the Appendix). This is a property that ATH shares with ALC (Franco and Hilker, 2013). In the remainder of this section, we consider two different measures of constancy stability, namely the fluctuation range and the fluctuation index.

3.1. Fluctuation range

The fluctuation range gives the upper and lower bounds of the population size, in between which the oscillations take place. It has been employed by Franco and Hilker (2013) to study stability properties of ALC. The smaller the fluctuation range, the more stable the population dynamics from the constancy point of view.

The ATH method can reduce the fluctuation range compared to the uncontrolled system. We illustrate this in Fig. 3a, where the fluctuation range decreases as the control intensity is increased. The figure suggests that ATH confines the population size within a region around the positive but unstable equilibrium K. The following theorem states that such a "trapping region" indeed exists and is completely determined by the map f and the control parameter c. The proof is provided in the Appendix.

Theorem 1. *Assume that (C1)–(C3) hold and $c \in (0, 1)$ is such that the activation threshold A_T exists. Then, applying ATH with intensity c confines the population sizes a_t for any $a_0 \in (0, b)$ within an interval $I_a = [l(c), u(c)]$ around the positive equilibrium K, with endpoints given by the expressions*

$$l(c) = \begin{cases} f(A_T/c), & d \le A_T, \\ f(f(d)), & d > A_T, \end{cases} \quad and \quad u(c) = \begin{cases} A_T/c, & d \le A_T, \\ f(d), & d > A_T. \end{cases} \tag{4}$$

If a specific goal is to be achieved, such as suppressing the population size below an upper limit; beyond a lower limit; or within two limits, the control intensity to achieve these goals can be determined. This is possible because the trapping region is completely determined by the map f and the control parameter.

The trapping region given in Theorem 1 is global, that is, the reduction of the fluctuation range does not depend on the initial condition. Fig. 3a shows a bifurcation diagram for ATH together with the limits of the intervals defining the trapping region given by Eq. (4). These intervals are sharp over a wide range of control parameters, which means that they cannot be improved for those parameter values.

ATH and ALC reduce the fluctuation range in different ways for the considered Ricker map. On the one hand, ALC asymptotically provides, for almost all control intensities, a lower limit for the population size that is clearly higher than the one observed for the uncontrolled system. The upper limit is significatively reduced for high intensities only, see Fig. 3b. On the other hand, ATH reduces the *upper* limit in comparison to the uncontrolled system over a wide range of control intensities, see Fig. 3a. The *lower* limit, however, increases significantly only for high control intensities.

Fig. 3a also shows the case when the control intensity c is greater than unity. This corresponds to harvesting a population that has decreased below rather than increased above a fraction of its previous size. Such a choice of control leads to extinction. The reason is that the harvesting always forces the population size to a fraction $1/c < 1$; as a consequence, there is no positive fixed point. Choosing a control intensity $c > 1$ for ALC leads the population to blow up (Fig. 3b). This is because the control forces the number of individuals to increase in each generation to at least the proportion $c > 1$ of its previous value.

Finally, we point out that we do not include the special case $c = 1$ in our analysis. In this case, the asymptotic behavior depends on the initial condition for both ATH and ALC, since there is a continuum of nontrivial equilibria—namely any population size greater than or equal to K, for ALC, or any population size less than or equal to K, for ATH. This has not been reported before.

3.2. Fluctuation index

In Fig. 3, we have seen that constancy stability measured in terms of the fluctuation range is always enhanced when ATH (or ALC) is applied to the Ricker model considered in this paper. Looking at another measure of constancy stability, namely the fluctuation index (FI), we will show that ATH does not always have a stabilizing effect.

The fluctuation index is a dimensionless measure of the average one-step variation of the population size scaled by the average population size in a certain period. It was introduced in Dey and Joshi (2006), and employed by Sah et al. (2013) and Franco and Hilker (2013) to study stability properties of ALC.

Mathematically, the FI is given by

$$FI = \frac{1}{T\bar{a}} \sum_{t=0}^{T-1} |a_{t+1} - a_t|, \tag{5}$$

a

b
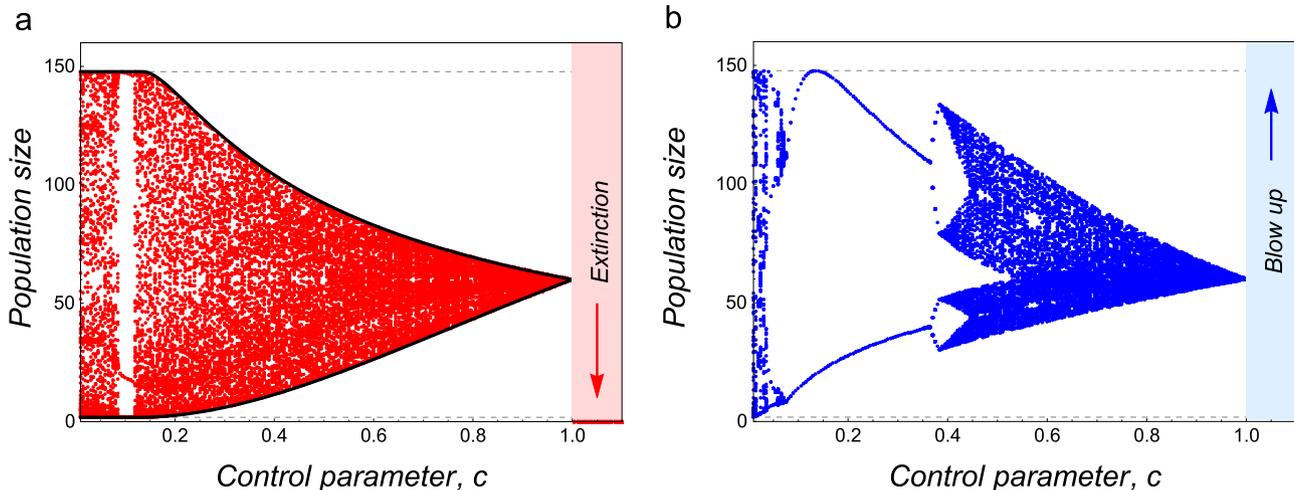
Fig. 3. (a) Bifurcation diagram for ATH. Red dots represent population sizes for the system (3) controlled by ATH. The bold black curves mark the limits of the intervals given by Eq. (4). (b) Bifurcation diagram for ALC with blue dots representing asymptotic population sizes. This diagram is analogous to Sah et al. (2013), except that we include the behavior for $c > 1$ and consider the correct underlying equation $a_{t+1} = \max\{f(a_t), c \cdot a_t\}$, cf. Franco and Hilker (2013). In both panels, the horizontal dashed lines mark the limits of the fluctuation range for the uncontrolled system. The diagrams are based on the Ricker map $f(x) = x \exp(r(1 - x/K))$ with $r = 3$ and $K = 60$, after removing transients. The initial population size is chosen as a pseudorandom number in $(0, f(d)]$. The diagrams do not include the behavior at $c = 1$, cf. the main text for details. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)
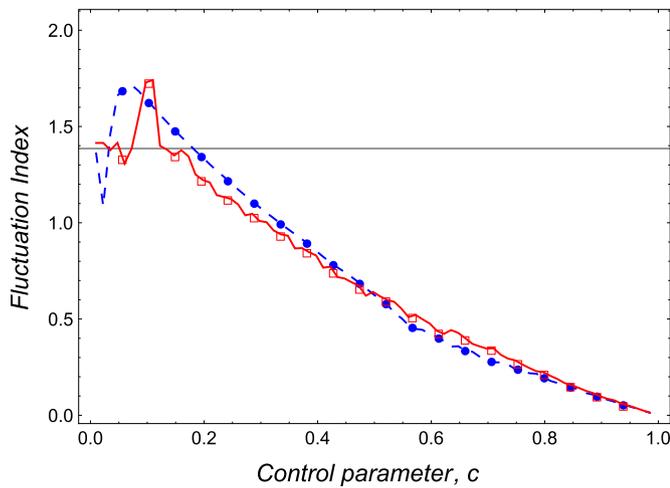
Fig. 4. Fluctuation indices (FIs) for the system controlled by ATH (red squares) and the system controlled by ALC (blue dots). The horizontal line marks the FI for the uncontrolled population. The dynamics of the uncontrolled population is described by the Ricker map $f(x) = x \exp(r(1 - x/K))$ with $r = 3$ and $K = 60$. The initial population size is chosen as a pseudorandom number in $(0, f(d))$, and the FI is obtained over 1000 generations after removing transients. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

Fig. 5. Mean yield per generation obtained by adaptive threshold harvesting. The dashed curve represents the asymptotic yield after discarding transients, and the solid curve represents the short-term yield including transients. Both yield values are averaged over 50 generations and over 1000 replicates with different initial conditions. The dynamics of the uncontrolled population are described by the Ricker map $f(x) = x \exp(r(1 - x/K))$ with $r = 3$ and $K = 60$. The initial population size is chosen as a pseudorandom number in $(0, f(d)]$ for the transient yield, and in the trapping region I_a for the asymptotic yield.

where $\bar{a}$ is the mean population size over a period of T time steps.

Fig. 4 shows that for small values of the control parameter, the FI of the system controlled by ATH can be greater than the FI of the uncontrolled system. The same holds true for ALC (Sah et al., 2013). For small values of the control intensity, the FI behaves quite erratically for both ATH and ALC, with pronounced peaks as well as sporadic drops below the baseline level set by the uncontrolled system. These sudden changes are due to attractor transitions, e.g. from chaos to periodic oscillations or between cycles of different periods (cf. Fig. 3).

For medium and high control intensities both ATH and ALC reduce the FI compared to the uncontrolled system. With a fixed value of the control intensity in this range, the effects of ATH and ALC on the FI are not only qualitatively but also quantitatively similar.

4. Yield

Control strategies usually come at a price. Previous papers measure this cost in terms of the "effort", i.e. the number of individuals added to or removed from a population (Hilker and Westerhoff, 2005; Dattani et al., 2011; Sah et al., 2013; Franco and Hilker, 2013; Tung et al., 2014). Here, we take a slightly different viewpoint and interpret the number of individuals removed as the yield. This seems to suggest itself since ATH is a harvesting method, provided that the population controlled is of some value. If the population is a pest, however, the term effort may be more fitting. In any case, we will consider two different ways of calculating the yield; one is based on the long-term dynamics and ignores transient effects (asymptotic yield), while the other is based on the short-term dynamics only and thus takes into account transients (transient yield). The reason for considering two measures of the yield is the following. For ALC, on the one hand, the asymptotic effort has been shown to decrease to zero if the control intensity approaches its maximum value (Sah et al., 2013). On the other hand, including transients can radically alter this observation and make the effort increase drastically (Franco and Hilker, 2013).

Fig. 5 shows the mean asymptotic yield per generation as a function of the ATH intensity. The curve has a hump-shaped form, reaching a maximum at some intermediate value of the control intensity. For too small control intensities, the yield is zero but then increases with c until the maximum is reached. For large control intensities beyond the maximum, the yield declines to zero as $c \to 1$.

Fig. 5 also shows the mean transient yield per generation, which is similar to the asymptotic yield for small and intermediate control intensities and reaches a local maximum, which is the same as for the asymptotic yield (Fig. 5). For large control intensities ($c > 0.85$), however, the transient yield increases steeply, blowing up as $c \to 1$.

The reason for this sharp increase in the yield are prolonged transients of the population dynamics if the control intensity is large. This has the effect that the population is repeatedly harvested—and, as a matter of fact, to a large degree. This not only increases the yield, but also extends the time it takes the system to reach the trapping region. The following section considers this in more detail.

5. Short-term behavior

In the previous section, we have seen that, in the short term, the mean yield per generation can differ greatly from the one in the long term. In certain circumstances, there is a long transient period before the population reaches its asymptotic behavior. During this transient, the short-term dynamics can be markedly different from the long-term dynamics with the desired properties (e.g., the mean yield or population size). Here, we show that ATH induces prolonged transient periods for rather large values of the control parameter. In the second part of this section, we propose an adjustment to the control rules that suppress prolonged transients and accelerate the controlled population to reach its long-term dynamics.

5.1. Transients in the controlled system

In order to quantify transients, we consider a value t_{max} that represents the maximum number of generations needed for the

a   b
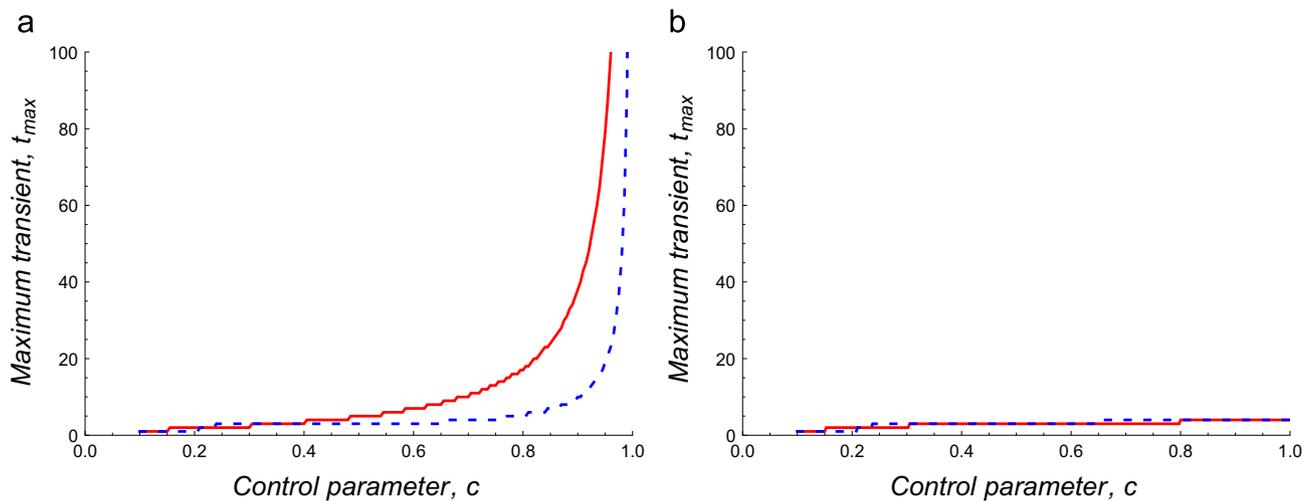
Fig. 6. (a) Maximum transients for ATH in solid red curve and for ALC in dashed blue curve. (b) Maximum transients for the adjusted version of ATH given by Eq. (6) in solid red curve and for the adjusted version of ALC given by Eq. (7) in dashed blue curve. The value t_{max} represents the maximum transient among all orbits with integer initial population size in the interval $(0, f(d)]$. The dynamics of the uncontrolled population are described by the Ricker map $f(x) = x \exp(r(1-x/K))$ with $K=60$ and $r=3$. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

population size to enter the trapping region, measured over all possible integer initial conditions in the interval $(0, f(d)]$. By taking the maximum, we take into account that transients depend on the initial condition, and we consider the 'worst case', i.e. the longest time it takes to reach the trapping region.

Fig. 6a shows that the maximum transient increases with the control intensity for both ATH and ALC. This increase is such that the maximum transients blow up near the maximum value of the control intensity, $c=1$. For medium and high control intensities ATH exhibits a longer maximum transient than ALC.

Example 1. For the Ricker map $f(x) = x \exp(r(1-x/K))$ with $K=60$ and $r=3$ the maximum transient t_{max} for ALC with intensity $c=0.95$ is 31 generations, whereas the corresponding value for ATH with the same intensity rises up to 134 generations.

Analyzing the causes of this behavior can help us to devise techniques for the cancellation of transients induced by ATH. Numerical simulations show that the maximum transients for ATH correspond to the largest values of the initial population size, a_0. The reason is that, due to the overcompensation in the population dynamics, the value $a_1 = f(a_0)$ is very small for large values of a_0 (see Fig. 2); the population size must then increase until entering the trapping region. However, the control slows down the population growth. In fact, for a sufficiently large value of a_0, we have $a_1 < A_T$. That is, harvesting control will be triggered in the next and successive generations during this transient period. In summary, the prolonged transients are due to repeated high-intensity harvesting of small population sizes. Since small population sizes can have a large production, the repeated high-intensity harvesting is also the reason why the transient yield increases sharply for large control intensities (cf. Fig. 5).

5.2. How to reduce transients

As the transient dynamics may last for a long time, an important question from the practical point of view is whether the system can be manipulated to reach its long-term behavior faster. One of the simplest solutions is probably to apply a perturbation such that the population size directly enters the trapping region. However, depending on the current population size, this requires that both restocking and culling can be implemented promptly and to a possibly large extent. Here we consider the situation that restocking is impossible (or very costly), so that, corresponding to

ATH, culling is the only possibility. We will propose an adjusted ATH method that cancels the prolonged transients without changing the asymptotic dynamics.

In the first part of this section, we have seen that the long transients are caused by repeated harvesting at small population sizes. The higher the control intensity, the more the population growth is slowed down and the longer it takes the population size to reach the trapping region. This effect can be avoided by the following two considerations.

1. We could stop harvesting small populations, say when the population size is below the trapping region. The lower limit of the trapping region is $l(c)$, but since the activation threshold A_T is always inside the trapping region, it would be actually sufficient to stop harvesting when the population size is smaller than $c \cdot l(c) < l(c)$. For any $a_t > c \cdot l(c)$, the population size in the next generation is $a_{t+1} = a_t/c > l(c)$.
2. However, a complete cessation of the harvesting might cause the population size to "jump" from one side of the trapping region to the other without entering it. Therefore, instead of completely canceling the harvesting of the small population sizes identified, we allow control but only to such a degree that the population size is not reduced below the trapping region.

All this leads to an adjusted ATH strategy with restricted harvesting at small population sizes, described by the following equation:

$$a_{t+1} = \begin{cases} \min\{f(a_t), a_t/c\}, & a_t > c \cdot l(c), & \text{(original ATH of large enough pop}^{\text{ns}}) \\ \min\{f(a_t), l(c)\}, & a_t \leq c \cdot l(c). & \text{(restricted harvesting of small pop}^{\text{ns}}) \end{cases}$$

(6)

This adjustment does not alter the asymptotic behavior of the controlled population because harvesting is only restricted when the population size is below the trapping region. Once it enters this region, the control follows the original ATH. We illustrate the improvement due to the adjustment (6) in Fig. 6b, which shows a significant reduction in maximum transients.

Example 2. The maximum transient in the system from Example 1 controlled by ATH with intensity $c=0.97$ lasts for 134 generations. With the adjustment given by (6), this transient decreases to only 4 generations.

The same kind of adjustment can be used to cancel prolonged transients generated by ALC. In that case, the restocking action of

the control lengthens transients when the population size is above the trapping region. For $a_t > u(c)$, where $u(c)$ denotes the upper limit of this region, the transient lasts until the population size decreases and enters the trapping region. Since the activation threshold is always inside the trapping region, restocking takes place in every generation of this stage, thus slowing down the decrease of the population size. The higher the control intensity, the more the population is restocked and the longer it takes for the population to decrease to the trapping region. As before, if the restocking control for population sizes above the trapping region were completely stopped, the population size could jump from one side of the trapping region to the other without entering it. The proper adjustment is therefore to restrict restocking to the upper limit $u(c)$. This leads to an adjusted version of ALC with restricted restocking at large population sizes described by the system

$$a_{t+1} = \begin{cases} \max\{f(a_t), c \cdot a_t\}, & a_t < c \cdot u(c), \quad \text{(original ALC of small enough pop}^{\text{ns}}\text{)} \\ \max\{f(a_t), u(c)\}, & a_t \geq c \cdot u(c). \quad \text{(restricted restocking of large pop}^{\text{ns}}\text{)} \end{cases}$$

(7)

As for ATH, this adjustment does not alter the asymptotic behavior of the controlled population because the restocking is only reduced when the population size is above the trapping region. Once the system is in the trapping region, the control follows the original ALC scheme.

Example 3. We consider the same uncontrolled population as in Examples 1 and 2. Applying ALC with restocking intensity $c = 0.97$ and for initial conditions a_0 that are integer values in $(0, f(d)]$, the maximum transient lasts 31 generations. With the adjustment given by (7), the maximum transient decreases to only 4 generations.

6. Model extensions

So far, we have seen how ATH can reduce erratic fluctuations in the population size for generic models with overcompensation. In this section, we extend the models to include different forms of noise, an Allee effect, and the lattice effect, i.e. integerization of population sizes. We will focus on the impact of these factors on the constancy stability promoted by ATH.

One way to include all three model extensions is a stochastic discrete-state difference equation of the form

$$a_{t+1} = \min\left\{ \left\lfloor f(a_t)I(a_t) \exp\left\{ \sigma \varepsilon_t - \frac{\sigma^2}{2} \right\} \right\rfloor, \lceil a_t/c \rceil \right\}, \tag{8}$$

where $f(a)$ is the production function and the minimum-operator models ATH with intensity c as before. There are three modifications. First, the factor $I(a)$ brings in positive density dependence to model a strong Allee effect. Here we assume $I(a) = sa/(1+sa)$, which represents the probability of finding a mate, with $s > 0$ measuring an individual's searching efficiency (Schreiber, 2003). Second, the flooring function $\lfloor a \rfloor$ maps a number to the greatest integer smaller than or equal to a, whereas the ceiling function $\lceil a \rceil$ maps a number to the smallest integer greater than or equal to a. This integerization takes into account that individuals always come and are harvested in whole numbers. Third, we include noise in the form of environmental stochasticity, where ε_t is a normally distributed variable with expectation 0 and variance 1, and σ is a parameter measuring the noise intensity.

The bifurcation diagram in Fig. 7a shows that ATH reduces the fluctuations in population size in a similar way like the deterministic, continuous-state model without Allee effect. Apart from the noisy appearance, the major difference is that too small populations go extinct. The fluctuation index is shown in Fig. 7b for different intensities of environmental stochasticities and different strengths of Allee effects. ATH is effective in reducing the fluctuation indices for the extended model over a similar range of control parameters as for the model without the extensions. Interestingly, it appears that control is less counterproductive at small values of c.

Another major source of noise in ecological systems is demographic stochasticity. This can be modeled in the following way (Brännström and Sumpter, 2006, cf.):

$$a_{t+1} = \min\left\{ \left\lfloor f(a_t)I(a_t) \exp\left\{ \sqrt{\frac{\sigma^2}{f(a_t)I(a_t)}} \varepsilon_t - \frac{\sigma^2}{2f(a_t)I(a_t)} \right\} \right\rfloor, \lceil a_t/c \rceil \right\},$$

(9)

where all the variables have the same meaning as before. The results in terms of population fluctuations and fluctuation indices (Fig. 7c and d, respectively) are similar to the model with environmental stochasticity.

To summarize, the stabilizing effect of ATH seems to be robust against the lattice effect, Allee effect and both environmental and demographic noise, even if their intensity is high. Even though one might expect that noise increases fluctuations, the fluctuation index in the stochastic model with Allee and lattice effect is smaller than in the deterministic baseline model for some values of the control parameter. In this sense, the model extensions seem beneficial for stabilization.

For comparison, ALC has been shown to be robust against the lattice effect and noise as well (Sah et al., 2013). Allee effects were not considered, and noise was modeled in form of uniformly distributed random numbers added to the model parameter. However, if the threshold value is measured before intervention (ALCb), noise and the lattice effect can produce counterproductive effects of control that are related to multiple attractors (Franco and Hilker, 2014).

7. Discussion and conclusions

The original version of adaptive limiter control (ALC) as proposed by Sah et al. (2013) is based on restocking the population as control intervention. In this paper, we have shown that adaptive threshold harvesting (ATH), i.e. the harvesting version of adaptive limiter control (h-ALC), can also stabilize fluctuating population sizes. This extends the applicability of adaptive limiters to situations when culling is the only possible form of intervention. Moreover, adaptive limiters may also be used as a harvesting strategy, thus widening the approach of threshold harvesting.

7.1. Commonalities between ATH and ALC

ATH and ALC have the following properties in common. We begin by considering stabilization aspects. First, both control strategies confine the population size in an interval around the unstable fixed point of carrying capacity. This guarantees that population size fluctuations are bounded and means that booms and busts of a population become restricted. We provide analytical expressions for the lower and upper bounds, which correspond to minimum and maximum population sizes during the oscillations. We prove that, for sufficiently large control intensity, the range of population size fluctuation reduces with increased control intensity, meaning that the control strategy is effective with respect to reducing the extent of population cycle amplitudes. Hence, constancy stability tends to improve.

Second, the fluctuation index also becomes smaller with increased control intensity, provided the control is at least of intermediate strength. Hence, constancy stability improves. However, for smaller control intensities both ATH and ALC may

increase the fluctuation index compared to the uncontrolled population. Third, the carrying capacity itself does not become stabilized. It is only the fluctuation in population size, as measured by the fluctuation index or the range of possible population sizes from the peak to the trough, that reduces in magnitude or amplitude. Yet, for the Ricker model studied in this paper, the mean population size is, asymptotically, remarkably constant at the level of the carrying capacity, for all values of the control parameter $0 < c < 1$.

Hence, the stabilization properties of ATH are analogous to the ones of ALC (previously investigated in Sah et al., 2013; Franco and Hilker, 2013). This is not a straight-forward result; as pointed out in the introduction, there are other control strategies which can greatly differ in the behavior they trigger, depending on whether interventions either add or remove individuals.

Moreover, the length of transients and the yield (or effort, respectively) behave similarly as a function of the control intensity for ATH and ALC (for the latter, again, this has been previously investigated in Sah et al., 2013; Franco and Hilker, 2013).

7.2. Differences between ATH and ALC

While both ATH and ALC reduce the fluctuation range for the Ricker model studied in this paper, they affect the lower and upper bounds of population size fluctuation in different ways. This means that the peaks and troughs possible during populations fluctuations respond differently to a control strategy that is implemented more intensively. For intermediate control intensities ($c \in [0.4, 0.7]$), ATH tends to reduce the upper bound in a more pronounced way, whereas ALC tends to increase the lower bound more markedly (see Fig. 3). Hence, ATH appears more effective in avoiding outbreaks and ALC in preventing extinctions. For large control intensities ($c \in (0.7, 1)$), however, both control methods seem equally effective in assuring minimum and maximum population sizes. We ought to mention that population size is here measured after control. If the population were censused before control, the interventions could affect the fluctuation range and fluctuation index differently, as shown in Franco and Hilker (2013, 2014) for ALC.

There are other differences between ATH and ALC. They occur when the control intensities exceed values of unity. Note that this parameter range has not been considered before for ALC. Basically,
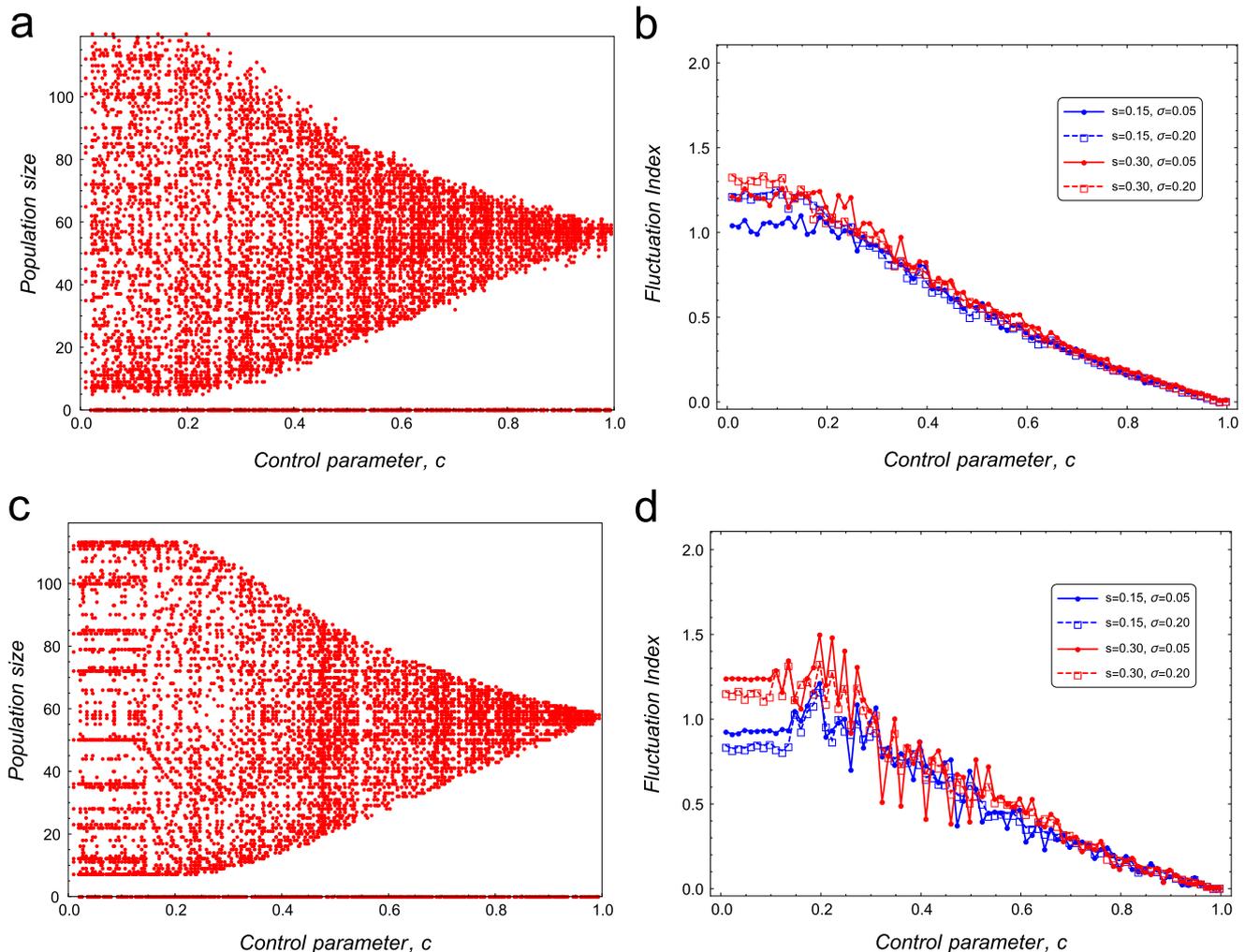
Fig. 7. Stabilization of population size fluctuations achieved by ATH in integerized stochastic models including a strong Allee effect. Top row: environmental stochasticity, based on Eq. (8). Bottom row: demographic stochasticity, based on Eq. (9). The left column shows asymptotic bifurcation diagrams for noise intensity $\sigma = 0.05$ and Allee effect strength $s = 0.15$ after removing transients. Initial population sizes are pseudorandom numbers in $(0, 5M/2)$, where M denotes the maximum of $f(x)l(x)$. The right column shows the fluctuation index as a function of the control parameter. The FI has been computed over 100 iterations (after rejecting 900 transients) and is averaged over 100 replicates. The production function is the Ricker model with $r = 3$ and $K = 60$.

$c > 1$ means restocking the population to levels larger than before a crash (ALC) and harvesting the population to a level smaller than before the increase in population size (ATH). As such, these are neither unrealistic parameter regimes nor senseless strategies. However, we find that these high control intensities drive the population extinct (ATH) or lead to unbounded population growth (ALC). Neither of which seems a desirable goal for the strategy considered.

We point out that the dynamics inside the trapping region are not theoretically analyzed in this study. Such an analysis seems an interesting line of research for which mathematical tools from Ergodic Theory could be useful.

7.3. Comparison with threshold harvesting

In contrast to adaptive limiters, threshold harvesting can actually stabilize the population dynamics to a stable equilibrium for sufficiently large control values (Glass and Zeng, 1994; Sinha, 1994). However, this comes at the cost of applying the intervention in every generation.

The other major difference is that, by definition, threshold harvesting affects only large population sizes. The long-term mean yield per generation tends to be a multimodal function of the threshold (cf. Fig. 3.9c in Hilker and Westerhoff, 2005). ATH, by contrast, is a harvesting policy that by its design is relevant also for populations with smaller sizes, provided they have grown sufficiently in comparison to the previous census. Interestingly, ATH shows a unimodal pattern in the long-term mean yield per generation (Fig. 5).

7.4. Yields and transients

While the primary goal of ATH is the stabilization of the fluctuations, it may also be applied as a harvesting strategy when the aim is to gain economic benefit from the exploited population. ATH may therefore represent an alternative to other harvesting strategies such as constant-effort, constant-yield, or threshold harvesting.

It turns out that we have to distinguish two situations, namely the long-term (asymptotic) and the short-term (transient) yield. Interestingly, the short-term yield gained by ATH rises sharply for values of high control intensities. That is, the yield becomes largest just before the population goes extinct for $c > 1$. The transition from a sustained population (with improved constancy stability and large yield) to extinction happens abruptly. In contrast to overexploitation with constant-effort harvesting, the collapse of the population does not take place gradually.

Trying to maximize the short-term gain is therefore risky in terms of sustainability. This bears some analogy to the observation that focusing on short-term gains can lead to dramatic consequences. One of the most prominent examples is probably the collapse of the cod stocks off of Newfoundland. Harvesting theory has therefore developed strategies for a sustainable catch, which can be considered as one of the cornerstones of mathematical bioeconomics (Clark, 1990). In fisheries, particular attention is paid to the maximum sustainable yield (MSY). Even though there are many concerns regarding the concept of MSY (e.g. Larkin, 1977; Ludwig et al., 1993), it remains a "key paradigm in fisheries management" (Maunder, 2008, p. 2295).

As a consequence, the harvesting literature has focused almost exclusively on long-term behavior and asymptotic yields. This is in contrast to the realization that harvesting represents additional perturbations to the population, and that the population rarely reaches its equilibrium state (Fox and Gurevitch, 2000). While transient dynamics are well-known to be important (Hastings, 2004), there is little work that aims to optimize harvest taking into account transient regimes (Jensen, 1996; Hauser et al., 2006; Koons et al., 2006, 2007). In stochastic population models, where population extinction is inevitable in the long run, Lande et al. (2003, p. 122) addressed this by considering the "expected cumulative yield over all time before eventual extinction of the population or reduction to a specific size". However, the time to stochastic population extinction may be quite long.

In this paper, we have shown that the yield can be markedly different, depending on whether we consider a short or long time scale. The dramatic increase in the short-term yield for large control intensities can be readily explained by the time it takes the population to reach the trapping region. During this time, the population is always harvested; the intervention frequency approaches 1 (not shown). That is, during this time the population effectively follows $a_{t+1} = a_t/c$ with c close to one, which corresponds to geometric growth with a rather slow per-capita production. Hence, due to the high yield from harvesting the population growth is significantly reduced and almost stopped.

Here, we have calculated the transient yield over a time horizon of 50 generations. This is arbitrary and could be varied.

7.5. Dealing with transients

The long transients that occur for high control intensities may appear quite desirable on the one hand because they increment the transient yield and simultaneously reduce the asymptotic fluctuation range. On the other hand, however, the prolonged transient period keeps the population size at low levels and prevents it from reaching the trapping region. In many practical situations, e.g. when it comes to supporting endangered species, it is imperative to reduce the transients.

A major drawback of adaptive limiters is that they trigger control actions whenever the population size exceeds (or falls below) a proportion of its magnitude in the preceding generation—regardless of whether this magnitude is close to zero (or on a high level, respectively). This can happen when the control intensity in both ATH and ALC is large. Yet, it does not seem to make sense to harvest a population that has increased in size when this size is still small and far below the trapping region. Similarly, for ALC, it seems unreasonable to restock a population that has declined but is still above the trapping region.

Based on this observation, we propose adjustments to both ATH and ALC that suppress prolonged transients, while retaining the asymptotic behavior. These adjustments concern only population sizes outside the trapping region and are such that the population size in the next generation does not 'overshoot' or 'undershoot' the trapping region. This is achieved by restricting the harvesting or restocking intervention for ATH and ALC, respectively. If the population size is within the trapping region, there is no need to alter the original control schemes because the population does not leave the trapping region. The adjustments work well (Fig. 6a, Examples 2 and 3) and are therefore effective in speeding up the transition from a transient period to the asymptotic regime.

As mentioned previously, transients are rarely taken into account or studied (but see Labra et al., 2003; Caswell, 2007; Ellis, 2013; Franco and Hilker, 2013; Franco and Ruiz-Herrera, 2015), even though they are ubiquitous in nature and may be actually more important than long-term dynamics (e.g. Hastings, 2004). The problem of directing an unstable or perturbed population in an efficient way to a desired state, such as the equilibrium, bears some analogy to the idea of targeting in chaos control (Kostelich, 1999; Hilker and Westerhoff, 2007b). In the ecological literature, we could not find many studies that investigate how to deal with transients. Harley and Manson (1981) suggested an "intermediate harvesting policy" for the transient period that accelerated the

transition to the equilibrium state of a structured population. Another, yet completely different approach is based on utilizing available time series; learning from 'trajectories from the past' one could steer the system to a desired state efficiently (Hilker and Westerhoff, 2007a,b).

This time-series-based approach has the advantage of not requiring any knowledge of the underlying laws of dynamics. As pointed out by Sah et al. (2013) for ALC, one of the main advantages of adaptive limiters over other strategies for controlling biological populations is that they can be implemented even when a good estimation of the population production map f for the uncontrolled system is not available. In this situation, the lack of knowledge about the system behavior makes it very difficult to reduce the length of transients. The adjusted methods presented here do require information on the upper or lower bounds of the trapping region.

Control strategies that are aimed at biological populations and that efficiently dealt with transient while requiring little information seem therefore an interesting research endeavor.

Acknowledgements

Appendix A. Proofs of the analytical results

Throughout this appendix, f^t refers to the tth iterate of f, i.e., $f^t = f \circ f^{t-1}$.

Proposition 1. *Assume that* (C1)–(C3) *hold. For control intensities* $c > \inf_{x \in (0,b)} x/f(x)$ *the set*

$$W = \{ x \in (0,b] : f(x) = x/c \}$$

is nonempty and has a maximum $A_T < K$. *If* $c \leq \inf_{x \in (0,b)} x/f(x)$ *the action of ATH is never triggered.*

Proof. Consider the functions $g(x) = x/f(x)$ and $h(x) = f(x) - x/c$. By (C2) we have $g(x) < 1$ in $(0,K)$ and $g(x) \geq 1$ in $[K,b)$, therefore the infimum of g can only correspond to its image at a point in $(0,K)$ (in that case, a minimum) or to its one-side limit on the right of 0. Assume that there exists $z \in (0,K)$ such that $\inf_{x \in (0,b)} g(x) = g(z) = z/f(z)$. Then, $c > z/f(z)$ and therefore $h(z) = f(z) - z/c > 0$. On the other hand, $f(K) = K < K/c$, and then $h(K) = f(K) - K/c < 0$. According to Bolzano's Theorem, there must exist a point $\tilde{x} > 0$ with $h(\tilde{x}) = 0$, and hence $\tilde{x} \in W$. Now we consider the case for which $\inf_{x \in (0,b)} g(x) = \lim_{x \to 0^+} g(x)$. Since $f(0) = 0$, the condition for the control parameter can be restated as

$$\frac{1}{c} < \lim_{x \to 0^+} \frac{1}{g(x)} = \lim_{x \to 0^+} \frac{f(x) - f(0)}{x} = f'(0^+).$$

By the linear approximation of f at $x = 0$ there exists a neighborhood $U \subset \mathbb{R}^+$ with $f(x) \approx f'(0^+) \cdot x > x/c$ for all $x \in U$. Therefore, $h(x) = f(x) - x/c > 0$ for all $x \in U$, and applying the same argument as before we can conclude that there must exist a point $\tilde{x} > 0$ with $h(\tilde{x}) = 0$, and hence $\tilde{x} \in W$. This completes the proof that W is nonempty for the considered control intensities.

Since f is strictly decreasing for $x > d$ and $f(K) = K$, we have that $W \subset (0,K)$. Moreover, the set $h^{-1}(\{0\}) \subset [0,b]$ is closed, and therefore $W = h^{-1}(\{0\}) \cap (0,b] \neq \varnothing$ has a maximum $A_T < K$.

Finally, for $c \leq \inf_{x \in (0,b)} x/f(x)$ it is $f(x) \leq x/c$ for all $x \in [0,b]$ and therefore $\min\{f(x), x/c\} = f(x)$. This means that the action of ATH is never triggered for these intensities. □

Corollary 1. *Assume that* (C1)–(C3) *hold and* $c \in (0,1)$ *is such that the activation threshold* A_T *exists. Then the map describing the dynamics of* a_t *for the controlled system under ATH with intensity* c,

$$H(x) = \min\{f(x), x/c\}, \tag{A.1}$$

verifies $H(x) = f(x)$ *for all* $x \geq A_T$ *and* $x \leq H(x) \leq x/c$ *for* $x \leq A_T$.

Proof. Since A_T is the highest intersection point between f and the straight line $y = x/c$, the inequality $f(x) \leq x/c$ must hold for all $x \geq A_T$. Hence, $H(x) = \min\{f(x), x/c\} = f(x)$ for these points. It is clear that $H(x) = \min\{f(x), x/c\} \leq x/c$. Since $A_T < K$ and $f(x) > x$ for all $x < K$, then $f(x) > x$ for all $x \leq A_T < K$. Given that $c < 1$ it is $x/c \geq x$ for all $x \geq 0$, and hence $H(x) = \min\{f(x), x/c\} \geq x$ for all $x \leq A_T$. □

Corollary 2. *Assume that* (C1)–(C3) *hold and* $c \in (0,1)$ *is such that the activation threshold* A_T *exists. Then ATH does not act in generation* t *if* $a_{t-1} > A_T$.

Proposition 2. *Assume that* (C1)–(C3) *hold and that the fixed point* K *is unstable for the uncontrolled system* (1). *Then, independent of the magnitude of ATH,* $c \in (0,1)$, *the controlled system has no asymptotically stable equilibria.*

Proof. For $c \leq \inf_{x \in (0,b)} x/f(x)$ the control by ATH is never triggered and the dynamics of the uncontrolled and controlled systems are the same. By condition (C2), this system has only two fixed points $x = 0$ and $x = K$. Since $f(x) > x$ for $0 < x < K$, $x = 0$ is an unstable equilibrium. Under the assumption that K is also unstable, we conclude that the "controlled" system has no asymptotically stable equilibria.

For control intensities $c > \inf_{x \in (0,b)} x/f(x)$ the dynamics of the controlled system by ATH are different from the ones for the uncontrolled system and are strictly given by (A.1). Looking at this map, it becomes clear that $x = 0$ is a fixed point. Since $c < 1$, we have that fixed points with $x > 0$ must verify $x = f(x)$, and thus $x = K$. Hence, the system controlled by ATH with intensity $c > \inf_{x \in (0,b)} x/f(x)$ has only two fixed points, namely 0 and K. We are going to prove that none of them is asymptotically stable. Consider the neighborhood $U = (0, A_T)$ of 0. We are going to prove that all orbits starting in U eventually leave it. Assume $a_t \in U$ for all $t \geq 0$. By Corollary 1 it is $H(x) > x$ for $x \in (0, A_T)$, which means $a_{t+1} > a_t$. Hence, the sequence $(a_t)_{t \in \mathbb{N}}$ is increasing and upper bounded, so it converges to some point $x^\star \in (0, A_T]$. This point is a fixed point of the system, which is absurd because there is no fixed point in the interval $(0, A_T] \subset (0, K)$. Hence, we conclude that 0 is an unstable fixed point.

Let us now prove that K is also unstable. As f is continuous and $f(K) = K < K/c$, there exists a neighborhood V of K such that $f(x) < x/c$ for all $x \in V$. Assume $a_t \in V$ for all $t \geq 0$. According to (A.1) it is $a_{t+1} = f(a_t)$ for all $t \geq 0$, and thus $a_t = f^t(a_0)$. Since K is an unstable fixed point for the uncontrolled system, this last equality contradicts our hypothesis and allows us to conclude that K is an unstable fixed point for the controlled system by ATH.

Theorem 2. *Assume that* (C1)–(C3) *hold and* $c \in (0,1)$ *is such that the activation threshold* A_T *exists. Then, applying ATH with intensity* c *confines the population sizes* a_t *for any* $a_0 \in (0,b)$ *into an interval* $I_a = [l(c), u(c)]$ *around the positive equilibrium* K, *with endpoints given by the expressions*

$$l(c) = \begin{cases} f(A_T/c), & d \leq A_T, \\ f(f(d)), & d > A_T, \end{cases} \quad and \quad u(c) = \begin{cases} A_T/c, & d \leq A_T, \\ f(d), & d > A_T. \end{cases}$$

Proof. In order to cover all possible expressions for I_a, we must consider two cases.

We start considering the case $d \leq A_T$, for which $I_a = [f(A_T/c), A_T/c]$. We have that $d \leq A_T < A_T/c$, and thus $f(d) \geq f(A_T) > f(A_T/c)$ because $c < 1$ and f is strictly decreasing in (d,b). From this, we conclude that the interval I_a has nonempty interior because $f(A_T)$

$= A_T/c$ and therefore $A_T/c > f(A_T/c)$. To prove that orbits enter I_a after an initial transient, we consider exhaustive and disjoint cases depending on the initial population size $a_0 \in (0, b)$.

1. Firstly, we assume $a_0 \in [A_T, A_T/c]$. In this case,

$$d \leq A_T \leq a_0 \leq A_T/c,$$

and thanks to the strict decrease of f on (d, b) we conclude that

$$f(d) \geq f(A_T) \geq f(a_0) \geq f(A_T/c).$$

On the other hand, according to Corollary 1, it is $a_1 = H(a_0) = f(a_0)$. With this, given that $f(A_T) = A_T/c$, we have that $A_T/c \geq a_1 \geq f(A_T/c)$ and thus $a_1 \in I_a$.

2. Next, we assume $a_0 \in (0, A_T)$. We are going to show that there exists $t_0 \in \mathbb{N}$ such that $a_{t_0} \in [A_T, A_T/c]$. Assume $a_t \notin [A_T, A_T/c]$ for all t. Let us prove by induction on t that $a_t \in (0, A_T)$ for all t. For $t = 0$ this condition is straightforward from the hypothesis of the case. Suppose $a_t \in (0, A_T)$ for certain $t \geq 1$. Since $a_t < A_T$, we have that $a_{t+1} = H(a_t) \leq a_t/c$ by Corollary 1, and therefore

$$a_{t+1} \leq a_t/c < A_T/c.$$

As $a_{t+1} \notin [A_T, A_T/c]$ by hypothesis, we conclude that $a_{t+1} \in (0, A_T)$. In conclusion, $a_t \in (0, A_T)$ for all t. By Corollary 1 it is $a_{t+1} = H(a_t) > a_t$ for all t, and hence the sequence $(a_t)_{t \in \mathbb{N}}$ is increasing and upper bounded by A_T, so it converges to some point $x^\star \in (0, A_T]$. This point must be a fixed point for the system, what is absurd because there is no fixed point in the interval $(0, A_T] \subset (0, K)$. In summary, we conclude that there exists $t_0 \in \mathbb{N}$ such that $a_{t_0} \in [A_T, A_T/c]$ and thus $a_{t_0+1} \in I_a$ by the first subcase.

3. Finally, we assume $a_0 \in (A_T/c, b)$. We have that $x_0 > A_T/c > A_T \geq d$ and according to Corollary 1, $a_1 = H(a_0) = f(a_0)$. From the strict decrease of f on (d, b) we conclude that

$$a_1 = f(a_0) < f(A_T/c) < f(A_T) = A_T/c,$$

what leads to one of the previous subcases and proves that orbits eventually enter I_a.

So far, we have proved that orbits enter the trapping region after a finite number of generations. To prove that they never leave it, we must see that $a_{t+1} \in I_a$ for $a_t \in I_a$. Assume $a_t \in I_a$ for certain t. If $f(A_T/c) \geq A_T$ we have that $A_T \leq f(A_T/c) \leq a_t \leq A_T/c$, and therefore $a_{t+1} \in I_a$ by the previous subcase 1. For $f(A_T/c) < A_T$ we consider two cases. If $a_t < A_T$ it is $a_t < a_{t+1} = H(a_t) < a_t/c$ (Corollary 1) and thus $A_T/c > a_t/c > a_{t+1} > a_t \geq f(A_T/c)$, what implies $a_{t+1} \in I_a$. If $a_t \geq A_T$ it is $a_t \in [A_T, A_T/c]$, and therefore $a_{t+1} \in I_a$ by the previous subcase 1.

We consider now the case $d > A_T$, for which $I_a = [f^2(d), f(d)]$. If $f^2(d) = f(d)$ then $f(d) > K$ is a fixed point for f, in contradiction with condition (C2). Hence, I_a has nonempty interior and we can proceed to prove that orbits enter this interval after a finite number of generations. To do this, we must distinguish some cases as before.

1. Firstly, we assume that $a_0 \in [d, f(d)]$. As $a_0 \geq d > A_T$, it is $a_1 = H(a_0) = f(a_0)$ by Corollary 1. Given that f is strictly decreasing on (d, b), from the inequality $d \leq a_0 \leq f(d)$ we deduce that $f^2(d) \leq f(a_0) = a_1 \leq f(d)$, what implies $a_1 \in I_a$.

2. Next, we assume $a_0 \in (0, d)$. We are going to see that there exists $t_0 \in \mathbb{N}$ such that $a_{t_0} \in [d, f(d)]$. Suppose $a_t \notin [d, f(d)]$ for all t. Given that f reaches its absolute maximum at $x = d$, for all $x \in [0, b]$ we have that $H(x) = \min\{f(x), x/c\} \leq f(x) \leq f(d)$. Hence, $a_t = H(a_{t-1}) \leq f(d)$ for all t, what together with $a_t \notin [d, f(d)]$ leads to conclude that $a_t \in (0, d)$ for all t. Since $f(x) > x$ for all $x \in (0, d) \subset (0, K)$ we have that $f(a_t) > a_t$ for all t, and given that $a_t/c > a_t$ it is $a_{t+1} = H(a_t) = \min\{f(a_t), a_t/c\} > a_t$. Hence, the sequence $(a_t)_{t \in \mathbb{N}}$ is increasing and upper bounded by d, so it converges to some point $x^\star \in (0, d]$. This point must be a fixed point for the system, what is absurd because there is no fixed point in the interval

$(0, d] \subset (0, K)$. We conclude that there exists $t_0 \in \mathbb{N}$ such that $a_{t_0} \in [d, f(d)]$ and, with this, $a_{t_0+1} \in I_a$ by the previous subcase.

3. Finally, we assume $a_0 \in (f(d), b)$. In this case we have that $0 < a_1 = H(a_0) \leq f(d)$ because $H(x) \leq f(d)$ for all $x \in (0, b)$. This brings us back to one of the previous cases and allows us to assert that orbits eventually enter the trapping region.

Now we proceed to prove the invariance of the trapping region under ATH. To do this, we assume $a_t \in I_a$ for a certain t and prove $a_{t+1} \in I_a$. We have seen that $a_{t+1} = H(a_t) \leq f(d)$ for all t, so it is enough to prove that $a_{t+1} \geq f^2(d)$. For $a_t \geq d$ this condition is straightforward from the previous subcase 1. If $a_t < d$ we have that $f(a_t) > a_t$ by condition (C2), and then

$$a_{t+1} = H(a_t) = \min\{f(a_t), a_t/c\} \geq \min\{a_t, a_t/c\} = a_t \geq f^2(d). \quad \square$$

References

Bellows, T., 1981. The descriptive properties of some models for density dependence. J. Anim. Ecol. 50, 139–156.

Brännström, À., Sumpter, D.J., 2006. Stochastic analogues of deterministic single-species population models. Theor. Popul. Biol. 69, 442–451.

Carmona, P., Franco, D., 2011. Control of chaotic behaviour and prevention of extinction using constant proportional feedback. Nonlinear Anal.: Real World Appl. 12 (6), 3719–3726.

Caswell, H., 2007. Sensitivity analysis of transient population dynamics. Ecol. Lett. 10 (1), 1–15.

Clark, C.W., 1990. Mathematical Bioeconomics. The Optimal Management of Renewable Resources. J. Wiley, New York.

Corron, N.J., Pethel, S.D., Hopper, B.A., 2000. Controlling chaos with simple limiters. Phys. Rev. Lett. 84, 3835–3838.

Cull, P., 1981. Global stability of population models. Bull. Math. Biol. 43 (1), 47–58.

Dattani, J., Blake, J.C., Hilker, F.M., 2011. Target-oriented chaos control. Phys. Lett. A 375 (45), 3986–3992.

Desharnais, R.A., Costantino, R., Cushing, J., Henson, S.M., Dennis, B., 2001. Chaos and population control of insect outbreaks. Ecol. Lett. 4 (3), 229–235.

Dey, S., Joshi, A., 2006. Stability via asynchrony in drosophila metapopulations with low migration rates. Science 312 (5772), 434–436.

Ditto, W.L., Sinha, S., 2015. Exploiting chaos for applications. Chaos 25 (9), 097615.

Ellis, M.M., 2013. Evidence for transient dynamics in plant populations based on long-term demographic data. J. Ecol. 101 (3), 734–742.

Fox, G.A., Gurevitch, J., 2000. Population numbers count: Tools for near-term demographic analysis. Am. Nat. 156, 242–256.

Franco, D., Hilker, F.M., 2013. Adaptive limiter control of unimodal population maps. J. Theor. Biol. 337 (0), 161–173.

Franco, D., Hilker, F.M., 2014. Stabilizing populations with adaptive limiters: prospects and fallacies. SIAM J. Appl. Dyn. Syst. 13 (1), 447–465.

Franco, D., Perán, J., 2013. Stabilization of population dynamics via threshold harvesting strategies. Ecol. Complex. 14, 85–94.

Franco, D., Ruiz-Herrera, A., 2015. To connect or not to connect isolated patches. J. Theor. Biol. 370, 72–80.

Fryxell, J., Smith, I., Lynn, D., 2005. Evaluation of alternate harvesting strategies using experimental microcosms. Oikos 111 (1), 143–149.

Glass, L., Zeng, W., 1994. Bifurcations in flat-topped maps and the control of cardiac chaos. Int. J. Bifurc. Chaos 4, 1061–1067.

Grimm, V., Wissel, C., 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109 (3), 323–334.

Güémez, J., Matías, M., 1993. Control of chaos in unidimensional maps. Phys. Lett. A 181 (1), 29–32.

Gueron, S., 1998. Controlling one-dimensional unimodal population maps by harvesting at a constant rate. Phys. Rev. E 57 (3), 3645.

Harley, P.J., Manson, G.A., 1981. Harvesting strategies for age-stable populations. J. Appl. Ecol. 18, 141–147.

Hassell, M., 1975. Density-dependence in single-species populations. J. Anim. Ecol. 44 (1), 283–295.

Hastings, A., 2004. Transients: the key to long-term ecological understanding?. Trends Ecol. Evol. 19, 39–45.

Hauser, C.E., Cooch, E.G., Lebreton, J.-D., 2006. Control of structured populations by harvest. Ecol. Model. 196, 462–470.

He, X.-Z., Westerhoff, F.H., 2005. Commodity markets, price limiters and speculative price dynamics. J. Econ. Dyn. Control 29 (9), 1577–1596.

Hilker, F.M., Westerhoff, F.H., 2005. Control of chaotic population dynamics: Ecological and economic considerations. Beitr. Inst. Umweltsystemforschung 32, 1–21.

Hilker, F.M., Westerhoff, F.H., 2006. Paradox of simple limiter control. Phys. Rev. E 73 (5), 052901.

Hilker, F.M., Westerhoff, F.H., 2007a. Preventing extinction and outbreaks in chaotic populations. Am. Nat. 170, 232–241.

Hilker, F.M., Westerhoff, F.H., 2007b. Triggering crashes in chaotic dynamics. Phys. Lett. A 362, 407–411.

Hudson, P.J., Dobson, A.P., 2001. Harvesting unstable populations: red grouse *Lagopus lagopus scoticus* (Lath.) in the United Kingdom. Wildl. Biol. 7, 189–195.

Hudson, P.J., Dobson, A.P., Newborn, D., 1998. Prevention of population cycles by parasite removal. Science 282, 2256–2258.

Jensen, A.L., 1996. Density-dependent matrix yield equation for optimal harvest of age-structured wildlife populations. Ecol. Model. 88, 125–132.

Koons, D.N., Rockwell, R.F., Grand, J.B., 2006. Population momentum: implications for wildlife management. J. Wildl. Manag. 70, 19–26.

Koons, D.N., Rockwell, R.F., Grand, J.B., 2007. Population inertia and its sensitivity to changes in vital rates and population structure. Ecology 88, 2857–2867.

Korpimäki, E., Norrdahl, K., 1998. Experimental reduction of predators reverses the crash phase of small-rodent cycles. Ecology 79, 2448–2455.

Kostelich, E.J., 1999. Targeting in chaotic dynamical systems. In: Schuster, H.G. (Ed.), Handbook of Chaos Control. Wiley-VCH Verlag, Weinheim. pp. 141–156.

Labra, F.A., Lagos, N.A., Marquet, P.A., 2003. Dispersal and transient dynamics in metapopulations. Ecol. Lett. 6 (3), 197–204.

Lande, R., Engen, S., Sæther, B.-E., 1995. Optimal harvesting of fluctuating populations with a risk of extinction. Am. Nat. 145, 728–745.

Lande, R., Engen, S., Sæther, B.-E., 2003. Stochastic Population Dynamics in Ecology and Conservation. Oxford University Press, Oxford.

Lande, R., Sæther, B.-E., Engen, S., 1997. Threshold harvesting for sustainability of fluctuating resources. Ecology 78, 1341–1350.

Larkin, P.A., 1977. An epitaph for the concept of maximum sustained yield. Trans. Am. Fish. Soc. 106, 1–11.

Liz, E., 2010. How to control chaotic behaviour and population size with proportional feedback. Phys. Lett. A 374 (5), 725–728.

Ludwig, D., Hilborn, R., Walters, C., 1993. Uncertainty, resource exploitation, and conservation: lessons from history. Science 260 17, 36.

Maunder, M.N. 2008, Maximum sustainable yield. In: Jorgensen, S.E., Fath, B. (Eds.), Encyclopedia of Ecology. Academic Press, Oxford. pp. 2292–2296.

May, R.M., 1976. Simple mathematical models with very complicated dynamics. Nature 261 (5560), 459–467.

McCallum, H., 1992. Effects of immigration on chaotic population dynamics. J. Theor. Biol. 154 (3), 277–284.

Parthasarathy, S., Sinha, S., 1995. Controlling chaos in unidimensional maps using constant feedback. Phys. Rev. E 51 (6), 6239–6242.

Ricker, W.E., 1954. Stock and recruitment. J. Fish. Board Can. 11 (5), 559–623.

Sah, P., Dey, S., 2014. Stabilizing spatially-structured populations through adaptive limiter control. PLoS ONE 9 (8), e105861.

Sah, P., Salve, J.P., Dey, S., 2013. Stabilizing biological populations and metapopulations through adaptive limiter control. J. Theor. Biol. 320, 113–123.

Schreiber, S.J., 2001. Chaos and population disappearances in simple ecological models. J. Math. Biol. 42 (3), 239–260.

Schreiber, S.J., 2003. Allee effects, extinctions, and chaotic transients in simple population models. Theor. Popul. Biol. 64, 201–209.

Singer, D., 1978. Stable orbits and bifurcation of maps of the interval. SIAM J. Appl. Math. 35 (2), 260–267.

Sinha, S., 1994. Unidirectional adaptive dynamics. Phys. Rev. E 49, 4832–4842.

Sinha, S., Parthasarathy, S., 1996. Unusual dynamics of extinction in a simple ecological model. Proc. Natl. Acad. Sci. 93 (4), 1504–1508.

Solé, R.V., Gamarra, J.G., Ginovart, M., López, D., 1999. Controlling chaos in ecology: From deterministic to individual-based models. Bull. Math. Biol. 61 (6), 1187–1207.

Stone, L., Hart, D., 1999. Effects of immigration on the dynamics of simple population models. Theor. Popul. Biol. 55 (3), 227–234.

Tung, S., Mishra, A., Dey, S., 2014. A comparison of six methods for stabilizing population dynamics. J. Theor. Biol. 356 (0), 163–173.

Wagner, C., Stoop, R., 2001. Optimized chaos control with simple limiters. Phys. Rev. E 63 017201-1–2.