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Adaptive limiter control of unimodal population maps

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HIGHLIGHTS

- We give theoretical support to recent experimental findings.
- Adaptive limiter control can be a global method to stabilize population oscillations.
- Our analytical results provide guidance how to choose the control intensity.
- The initial transients can be important and inflate the control effort.
- We present new properties with important practical implications.

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ABSTRACT

We analyse the adaptive limiter control (ALC) method, which was recently proposed for stabilizing population oscillations and experimentally tested in laboratory populations and metapopulations of *Drosophila melanogaster*. We thoroughly explain the mechanisms that allow ALC to reduce the magnitude of population fluctuations under certain conditions. In general, ALC is a control strategy with a number of useful properties (e.g. being globally asymptotically stable), but there may be some caveats. The control can be ineffective or even counterproductive at small intensities, and the interventions can be extremely costly at very large intensities. Based on our analytical results, we describe recipes how to choose the control intensity, depending on the range of population sizes we wish to target. In our analysis, we highlight the possible importance of initial transients and classify them into different categories.

1. Introduction

Stability of biological populations has attracted a lot of attention because it determines, amongst others, extinction probability (Thomas et al., 1980; Berryman and Millstein, 1989; Allen et al., 1993), effective population sizes and genetic diversity (Mueller and Joshi, 2000) as well as population fitness (Charlesworth, 1994). A large range of fluctuation in the population size over time tends to invoke a low stability of the population. Several authors have therefore proposed control strategies to stabilize a population (e.g. McCallum, 1992; Solé et al., 1999; Stone and Hart, 1999; Hilker and Westerhoff, 2006, 2007a; Liz, 2010; Carmona and Franco, 2011; Dattani et al., 2011; Franco and Perán, 2013). These control strategies typically aim at creating stable population sizes by removing (harvesting/thinning) or adding (stocking) individuals following certain rules. Although the mechanisms of these strategies are theoretically well understood, experimental demonstration of reduced population fluctuations remains rare (Desharnais et al., 2001; Becks et al., 2005; Dey and Joshi, 2007, 2013) and there is, in general, a lack of empirical evidence for the stabilizing properties of control methods.

Recently, Sah et al. (2013) have proposed adaptive limiter control (ALC) as a novel method for controlling population oscillations. The idea behind ALC is to restock the population if there is too large a crash in the population size. More specifically, individuals are added if the population size falls below a certain fraction of its value in the previous generation. ALC is related to the family of limiter control methods (see the next section for a more detailed description of the method). Sah et al. (2013) have tested ALC in experiments with laboratory populations and metapopulations of the fruit fly *Drosophila melanogaster*. Their results suggest that increased ALC intensity enhances population stability, measured in terms of reduced fluctuations and extinction frequencies.

ALC is in some sense 'atypical' when compared to other control methods, because it is one of the few methods that have been

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studied empirically. Sah et al. (2013) corroborate their experimental results also by some numerical simulations of a mathematical model. However, it is inherent to the method of numerical simulations that they only apply to particular situations, specified for example by the values of model parameters and initial conditions. It is not clear whether results observed for some simulations will hold for other simulations. For instance, we support the observation of Sah et al. (2013) that in some situations ALC is not only ineffective, but actually worsens population stability. Hence, the question arises whether or not, and under which circumstances, ALC is a good strategy to stabilize biological populations.

In this paper, we present mathematically rigorous results on ALC. They provide a theoretical basis for the stabilizing properties observed in the experiments and simulations by Sah et al. (2013). Currently, there is a lack in the theoretical understanding of ALC, as there are no results available that explain the mechanisms and effects of ALC. Our analytical results thus contribute to filling this gap.

In the next section, we begin with introducing ALC in a simple deterministic setting. We then present a number of analytical results. The main one confirms the observation of Sah et al. (2013) that greater ALC intensities invoke the population to have lower variation in size over time, measured in terms of the fluctuation range. In addition, we present a number of novel results. We work out a number of useful properties that can be relevant for the implementation and applicability of ALC. This includes the frequency and the cost of interventions; a description of initial transients; how to plan ahead; and how to choose the ALC intensity in order to attain a certain desired reduction in the fluctuation magnitude. Moreover, we show that the stabilizing effect of ALC is global, i.e. independent of the initial population size, for a wide range of population models.

2. Adaptive limiter control

2.1. Underlying population dynamics

Before introducing the ALC method and some of its effects, we describe the underlying population dynamics in the absence of control. We assume that the uncontrolled population follows the discrete-time dynamical system given by

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

where x_t denotes the population size at time step t. Function f describes the population production, sometimes also called the stock–recruitment curve, and is assumed to satisfy the following conditions:

(C1) $f : [0, b] \to [0, b)$ ($b = \infty$ is allowed) is continuously differentiable and such that $f(0) = 0$ and $f(x) > 0$ for all $x \in (0, b)$.
(C2) f has two nonnegative 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 $d < K$ in such a way that $f'(x) > 0$ for all $x \in (0, d)$, $f'(x) < 0$ for all $x > d$, and $f'(0^+), f'(b^-) \in \mathbb{R}$.

These conditions are standard assumptions in the study of discrete-time population dynamics (e.g. May, 1976; Singer, 1978; Cull, 1981; Schreiber, 2001; Liz, 2007; Carmona and Franco, 2011). Essentially, they describe a hump-shaped population production (peaking at $x=d$). From a biological point of view, the population dynamics are overcompensatory, caused e.g. by scramble competition (Britton, 2003). The population has two fixed points, namely the extinction state $x=0$ and a positive equilibrium $x=K$. There is no demographic Allee effect. Examples include the Ricker (1954), Hassell (1975) and generalized Beverton–Holt (Bellows, 1981) maps, in their overcompensatory regimes where applicable.

2.2. Modelling ALC

If the population size x_t at time step t drops below a certain threshold, then there is an intervention augmenting the population back to this threshold. In this, ALC is similar to limiter control methods (Corron et al., 2000; Hilker and Westerhoff, 2005, 2006). Since the threshold is a fraction of the previous population size and as such variable, the limiter is considered 'adaptive'. In Fig. 1 we illustrate how ALC modifies the dynamics of the population. In particular, we can observe a reduction in the fluctuation range.

When applying ALC, we have two different population sizes at time step t, namely the population size before and after the action of ALC. In discrete-time models, the order of events is important (Åström et al., 1996; Bodine et al., 2012; Lutscher and Petrovskii, 2008). Let us denote by b_t (respectively a_t) the population size before (respectively after) the action of ALC in time step t. We note that $b_t \le a_t$, because ALC never removes individuals.

If ALC augments the population size, this induces an 'intra-generation' variation. We illustrate this in Fig. 1 with dashed red lines. In this example, we can observe that the sizes of b_t and a_t are different when ALC is applied.

A direct consequence of having two population sizes at time step t is that we must choose one of them to define the adaptive threshold in the next time step $t+1$. In their experiments and

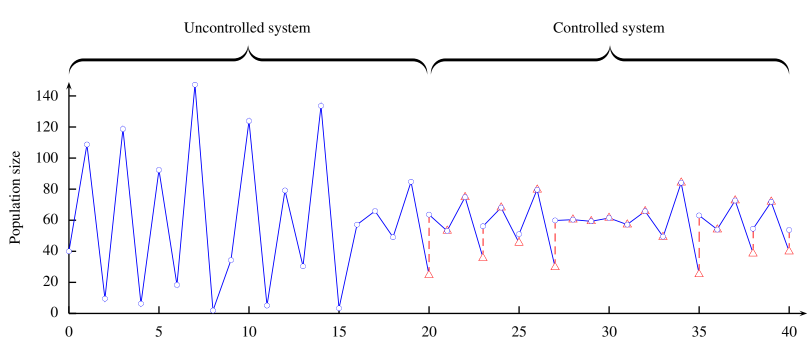

Fig. 1. During the first 20 generations, the population is uncontrolled and follows Eq. (1). In the next 20 generations, the population is controlled by ALC, following system (2). Blue circles and red triangles indicate the population size after and before ALC, respectively. Therefore, a blue circle inside a red triangle corresponds to a generation where ALC did not modify the population. Dashed lines connecting blue circles with red triangles indicate ALC interventions (thus inducing intra-generation variation). Note the clear reduction of the fluctuation range in the controlled population compared to the uncontrolled population. Population dynamics follow the Ricker map $f(x) = x\exp(r(1-x/K))$ with growth parameter $r=3$ and carrying capacity $K=60$. ALC is applied with intensity $c=0.75$. (For interpretation of the references to colour in this figure caption, the reader is referred to the web version of this paper.)