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A comparison of six methods for stabilizing population dynamics

Sudipta Tung, Abhishek Mishra, Sutirth Dey*

Population Biology Laboratory, Biology Division, Indian Institute of Science Education and Research-Pune, Dr. Homi Bhabha Road, Pune, Maharashtra 411008, India

HIGHLIGHTS

- Methods that involve culling promote persistence more than constancy stability.
- The converse is true for methods that involve only restocking steps.
- Efficacies of the methods depend upon growth rates and carrying capacities.
- Overall, restocking to a fixed lower threshold is the optimal control method.

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ABSTRACT

Over the last two decades, several methods have been proposed for stabilizing the dynamics of biological populations. However, these methods have typically been evaluated using different population dynamics models and in the context of very different concepts of stability, which makes it difficult to compare their relative efficiencies. Moreover, since the dynamics of populations are dependent on the life-history of the species and its environment, it is conceivable that the stabilizing effects of control methods would also be affected by such factors, a complication that has typically not been investigated. In this study, we compare six different control methods with respect to their efficiency at inducing a common level of enhancement (defined as 50% increase) for two kinds of stability (constancy and persistence) under four different life-history/environment combinations. Since these methods have been analytically studied elsewhere, we concentrate on an intuitive understanding of realistic simulations incorporating noise, extinction probability and lattice effect. We show that for these six methods, even when the magnitude of stabilization attained is the same, other aspects of the dynamics like population size distribution can be very different. Consequently, correlated aspects of stability, like the amount of persistence for a given degree of constancy stability (and vice versa) or the corresponding effective population size (a measure of resistance to genetic drift) vary widely among the methods. Moreover, the number of organisms needed to be added or removed to attain similar levels of stabilization also varies for these methods, a fact that has economic implications. Finally, we compare the relative efficiencies of these methods through a composite index of various stability related measures. Our results suggest that Lower Limiter Control (LLC) seems to be the optimal method under most conditions, with the recently proposed Adaptive Limiter Control (ALC) being a close second.

1. Introduction

1.1. Background

Since the seminal work of Ott, Grebogy and Yorke (Ott et al., 1990), a large number of methods have been proposed to stabilize the dynamics of unstable non-linear systems (for reviews see (Andrievskii and Fradkov, 2003, 2004; Scholl and Schuster, 2008)). Many of these methods work by manipulating the parameters of the system in real time, such that the trajectory of the system can be stabilized to the desired kind of dynamics (stable point or cycles of appropriate periodicity). However, such methods are unsuitable for controlling real biological populations in which the precise equations governing the system are typically unknown and parameters (e.g. intrinsic growth rate, carrying capacity, etc.) can only be estimated *a posteriori*, through model-fitting. Control of biological populations is more easily achieved through methods that stabilize the dynamics through perturbations to the state variable, (i.e. the population size) and require relatively less system-specific

* Corresponding author. Tel.: +91 20 25908054.
E-mail addresses: sudipta.tung@students.iiserpune.ac.in (S. Tung), amishra@students.iiserpune.ac.in (A. Mishra), s.dey@iiserpune.ac.in (S. Dey).

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information. Over the last two decades, many such methods have been proposed (Corron et al., 2000; Dattani et al., 2011; Hilker and Westerhoff, 2005, 2007; McCallum, 1992; Sah et al., 2013) and at least a few of them have also been empirically verified (Sah et al., 2013; Becks and Arndt, 2008; Desharnais et al., 2001; Dey and Joshi 2007).

This proliferation of biologically relevant control methods has created some interesting problems of its own. In ecology, there are multiple notions about the concept of stability (Grimm and Wissel, 1997) and ideally one would not like to opt for a method that enhances one kind of stability (say reduction in fluctuation in population size) at the cost of another (say long term persistence). However, studies on control methods often focus on enhancement of only one type of stability, without investigating how other aspects of the dynamics get affected (e.g. Corron et al., 2000; McCallum, 1992; Güémez and Matías, 1993)). Recent empirical studies indicate that induction of one kind of stability may (Sah et al., 2013) or may not (Dey et al., 2008) translate into the enhancement of other kinds of stability. Therefore it is important to investigate how different control methods affect multiple kinds of stability simultaneously.

Such comparisons can be quite complex as most theoretical studies employ different models of population growth and evaluate the efficacies of the control methods in different parameter ranges, some of which can even be biologically unrealistic. Thus, for meaningful comparison, these methods need to be investigated under common conditions, i.e. for the same model and similar levels of enhancement of stability. Moreover, since it has been empirically shown that the effects of perturbation can vary depending on the intrinsic growth rates or the environment of the population (e.g., (Dey and Joshi, 2013)), it is conceivable that the efficacy of control methods can also be affected by these factors. Thus, any comparison of the control methods also needs to take into account multiple combinations of intrinsic growth rate and carrying capacity values. Finally, any real world scenario typically involves an economic component (Hilker and Westerhoff, 2005), which might play a significant role in deciding which control method is best suited to a given scenario. Our study aims to compare the performance of six well-known control methods in population dynamics under the above-mentioned set of conditions.

Here, owing to logistic constraints, we restrict our analyses to six control methods which were selected based on two criteria. Our primary selection criterion was the relative ease with which the methods could be implemented in real, biological populations. This ruled out some of the well-known, empirically verified control methods that require extensive knowledge of the equations governing the system and the corresponding parameter values (Desharnais et al., 2001; Becks et al., 2005). Our second criterion was the extent of information already available about the control methods in the population dynamics literature. Barring one (Both Limiter Control, see Section 1.2), for which we found no prior reference in the literature, all the methods that we chose have been extensively investigated both analytically and numerically, and have been shown to be robust to at least some degree of noise. We realize that there might be other control methods that fit these two criteria and therefore do not claim that our coverage is comprehensive.

1.2. Description of six control methods

The mathematical expressions for the six control methods and the corresponding ranges investigated in the exploratory analysis are given in Table 1. Here we present a brief description of how these methods stabilize population dynamics. Among the six, constant pinning (CP), also referred to in the literature as constant immigration/feedback, is perhaps the most well studied (McCallum, 1992; Sinha and Parthasarathy, 1995; Solé et al., 1999) and involves the influx of a constant number of individuals (from some external source) into the population in every generation. In its general form, CP involves both immigration and emigration from a population (Sinha and Parthasarathy, 1995), but here we concentrate solely on immigration which has been shown to enhance stability for populations governed by the Ricker (Ricker, 1954) dynamics (McCallum, 1992; Stone, 1993). The reason for this is best understood graphically. For models that have single-humped first-return maps (also known as the stock-recruitment curve) with at most one inflection point to the right of the maximum, the nature of the dynamics depends upon how negative the slope of the first-return map is at the point where it intersects the 45° line. Since constant immigration shifts the entire return map upwards (see Fig. 2 of Stone and Hart (1999)), the slope at this point is reduced, which can convert chaotic dynamics into periodic oscillations or even stable points, depending upon the magnitude of the reduction (Sinha and Parthasarathy, 1995). For those models, such as the logistic, where moving up the first-return map increases the slope at the intersection point with the 45° line, CP destabilizes the dynamics by making it more complex (Sinha and Parthasarathy, 1995). Biologically, CP creates a “floor” and does not allow the population to hit values below the constant immigration threshold. This method has been empirically demonstrated to reduce fluctuations in sizes for spatially-unstructured (Dey and Joshi, 2013) but not spatially structured populations (Dey and Joshi, 2007).

One of the issues with constant pinning is that the population sizes are augmented even when they are not low. This problem is avoided with the so called hard ‘limiter control from below’ (Hilker and Westerhoff, 2005), or Lower Limiter Control (LLC) in this study, which prescribes that each time the population size falls below a pre-determined lower threshold, it is brought back to that value through restocking. Graphically, LLC truncates some part of the lower end of the return map, which in turn makes part

Table 1
Details of the six control methods compared in this study*.

Sl. no.	Control Method	Mathematical expression	Control parameter constants	Control parameter range(s) for Fig S1-S6	Step size
1.	Constant Pinning (CP)	$a_t = b_t + p$	Pin (p)	1 to $k-1$	1
2.	Lower Limiter Control (LLC)	$a_t = \max\ [b_t, h]$	Lower limit (h)	1 to $k-1$	1
3.	Adaptive Limiter Control (ALC)	$a_t = \max\ [b_t, c \times a_{t-1}]$	ALC intensity (c)	0.05–0.95	0.05
4.	Upper Limiter Control (ULC)	$a_t = \min\ [b_t, H]$	Upper limit (H)	$k+1$ to $3k$	1
5.	Both Limiter Control (BLC)	$a_t = \max\ [h, \min[b_t, H]]$	Lower limit (h)	1 to $k-1$	1
			Upper limit (H)	$k+1$ to $3k$	1
6.	Target Oriented Control (TOC)	$a_t = \max\ [0, c_d \times T + (1-c_d) \times b_t)]$	Target, T	k	NA
			c_d	0.05–0.95	0.05

* b_t and a_t are the population sizes before and after perturbation in the tth generation, such that $b_{t+1} = \text{FUNC}(a_t)$, where FUNC stands for the population recruitment function (Ricker model, in this study). For BLC, $H > h$. NA denotes not applicable.