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Stabilizing biological populations and metapopulations through Adaptive Limiter Control

Pratha Sah [1], Joseph Paul Salve, Sutirth Dey *

Population Biology Laboratory, Indian Institute of Science Education and Research-Pune, Biology Division, Pashan, Pune 411021, Maharashtra, India

HIGHLIGHTS

- ► Novel method for controlling the dynamics of populations/metapopulations.
- ► First control method empirically shown to work for a biological metapopulation.
- ► The method reduces both population fluctuations as well as extinction probability.
- ► Biologically realistic simulations indicate the results to be widely applicable.
- ► We provide empirical validation for various extant theoretical studies in this area.

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ABSTRACT

Despite great interest in techniques for stabilizing the dynamics of biological populations and metapopulations, very few practicable methods have been developed or empirically tested. We propose an easily implementable method, Adaptive Limiter Control (ALC), for reducing the magnitude of fluctuation in population sizes and extinction frequencies and demonstrate its efficacy in stabilizing laboratory populations and metapopulations of *Drosophila melanogaster*. Metapopulation stability was attained through a combination of reduced size fluctuations however, and synchrony at the subpopulation level. Simulations indicated that ALC was effective over a range of maximal population growth rates, migration rates and population dynamics models. Since simulations using broadly applicable, non-species-specific models of population dynamics were able to capture most features of the experimental data, we expect our results to be applicable to a wide range of species.

1. Introduction

Stabilizing the dynamics of unstable systems has been a major endeavor spanning different scientific disciplines. Unfortunately, most methods proposed in the literature require extensive *a priori* knowledge of the system and/ or real-time access to the system parameters (Schöll and Schuster, 2008). This typically makes such methods unsuitable for controlling biological populations that are often characterized by poor knowledge of the underlying dynamics (see Suárez, 1999) and inaccessibility of the system parameters. This problem was partly alleviated with the advent of methods that needed no *a priori* knowledge of the system and perturbed the state variables rather than the system parameters (Corron et al., 2000; Güémez and Matías, 1993; Hilker and Westerhoff, 2007). For example, at least in single-humped one-dimensional maps, constant immigration of sufficient magnitude in every generation can convert chaotic dynamics into limit cycles (McCallum, 1992). Similar phenomena of simpler dynamics replacing more complex behavior were also observed in models of more complex systems (e.g. Astrom et al., 1996; McCann and Hastings, 1997). However, very few of these theoretical predictions have been empirically verified till date. In one experiment, the dynamics of *Tribolium* populations were stabilized by low magnitude perturbations (Desharnais et al., 2001). This method required the empirical characterization of the chaotic strange attractor of the dynamics, followed by computation of local Lyapunov exponents over the entire attractor: a somewhat daunting proposition for most application-oriented purposes. Another empirical study on a chemostat-based three-species bacteria–ciliate prey–predator system, implemented theoretically calculated rates of dilution to convert chaotic dynamics into limit

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* Correspondence to: Biology Division, Indian Institute of Science Education and Research, 3rd floor, Central Tower, Sai Trinity Building, Garware Circle, Pashan, Pune-411 021, Maharashtra, India. Tel.: +91 20 25908054.

E-mail addresses: ps875@georgetown.edu (P. Sah), josephsalve@gmail.com (J. Paul Salve), s.dey@iiserpune.ac.in, deysutirth@gmail.com (S. Dey).

[1] Present address: Department of Biology, Georgetown University, 37th and O Streets NW, Washington, DC, USA

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cycles (Becks et al., 2005). Again, the calculations leading to the prediction of the dilution rates required fairly detailed system-specific modeling (see Becks et al. 2005 and references therein) and were implemented in spatially-unstructured populations.

One of the several complications with real populations is that they are very often spatially-structured (metapopulations), which can lead to complex patterns and dynamics (Cain et al., 1995; Maron and Harrison, 1997; Perfecto and Vandermeer, 2008; Turchin et al., 1998). Not surprisingly therefore, the dynamics of metapopulations have received wide attention, in the context of stabilization (e.g. Doebeli and Ruxton, 1997; Parekh et al., 1998). The rationale behind such studies was that if the dynamics of a fraction of the subpopulations in a metapopulation can be controlled in some way, then the stabilized subpopulations can alter the dynamics of their neighbors and so on. Thus one could expect a cascading effect through the metapopulation, ultimately leading to the stabilization of the global dynamics. However, the only study using localized perturbations on real, biological metapopulations failed to find any effect on global dynamics (Dey and Joshi, 2007). This was attributed to the effects of localized extinctions in the subpopulations, which were shown to render a previously proposed method (Parekh et al., 1998) ineffective in terms of stabilizing metapopulations. Thus, there are no known methods that have been empirically demonstrated to stabilize the dynamics of biological metapopulations.

One possible reason for this lack of empirical verification of proposed control methods might be related to the multiplicity of notions related to population stability in ecology. Even 15 years back, a review on the subject had cataloged no less than 163 definitions and 70 concepts pertaining to stability in the ecological literature (Grimm and Wissel, 1997). Most proposed control methods (Corron et al., 2000; Güémez and Matías, 1993; McCallum, 1992; Sinha and Parthasarathy, 1995; Solé et al., 1999) pertain to attainment of stability in the form of chaos being replaced by simpler dynamics (stable point or low periodicity limit cycles). While there have been a number of studies demonstrating chaos, or the lack there of, in empirical datasets (Becks and Arndt, 2008; Becks et al., 2005; Dennis et al., 1995; Hassell et al., 1976; Turchin and Taylor, 1992), many of the methods proposed for detecting chaos suffer from their own theoretical limitations (Becks et al., 2005; Turchin and Taylor, 1992). Moreover, the distinction between deterministic chaos and noisy limit cycles often does not lead to meaningful insights in terms of practical applications like resource management or reduction of the extinction probability of a population. Therefore, many experimental studies have concentrated on other attributes of stability that are relatively easier to determine, particularly in noisy systems. Two of the attributes of population stability often investigated in these contexts are the so called constancy (e.g. Mueller et al., 2000) and persistence (e.g. Ellner et al., 2001). A population is said to have greater constancy stability when it has a lower variation in size over time, while greater persistence stability simply refers to a lower probability of extinction within a given time frame (Grimm and Wissel, 1997). In this study, we empirically investigate both these attributes of population stability.

Here we propose a new method, which we call adaptive limiter control (ALC), for reducing the amplitude of fluctuation in population size over time. Our main motivation in proposing this method is to come up with a scheme that would be easy to implement, and at the same time, would be effective in terms of both constancy and persistence of spatially -unstructured and –structured populations. We first explore the method numerically and study its long-term behavior. We then use biologically realistic simulations (incorporating noise, extinction and lattice effect) over a range of biologically meaningful parameter values to demonstrate the efficacy of our method for populations with no migration (henceforth called single populations) as well as spatially-structured populations experiencing migration among the constituent subpopulations, henceforth called metapopulations (Hanski, 1999). We also report two separate experiments using replicate single populations and metapopulations of *Drosophila melanogaster* that validate our theoretical predictions. We further show that ALC reduces extinction in both single populations and metapopulations, albeit by different mechanisms. Finally, we compare ALC with other control methods in the literature, and point out why we believe ALC to be likely applicable to a wide range of organisms.

2. Adaptive Limiter Control (ALC)

Mathematically, ALC can be represented as:

$$\begin{aligned} N_{t+1} &= f(N_t) && \text{if } N_t \geq c \times N_{t-1}, \\ N_{t+1} &= \mathrm{f}(c \times N_{t-1}) && \text{if } N_t < c \times N_{t-1} \end{aligned}$$

where N_t represents the population size at generation t, $\mathrm{f}(N_t)$ is a function that predicts N_{t+1} for a given N_t, and c is the ALC parameter. In other words, when the population size in the current generation goes below a threshold, defined as a fraction c of the population size in the previous generation, individuals are added from outside to bring the number up to that threshold. No perturbations are made if the population size is above that threshold. The biological interpretation of this scheme is straightforward: the population size in the current generation (i.e. N_t) is not allowed to go below a fraction c of the previous population size (N_{t-1}). As the magnitude of the control is a function of the population size in the previous generation, the number of individuals added changes constantly. This adaptive nature of the algorithm makes it independent of the range of the size of the populations to be controlled, thus enhancing its applicability. ALC belongs to the so called "limiter control" family of algorithms (Corron et al., 2000; Hilker and Westerhoff, 2006; Zhou, 2006), although to the best of our knowledge, this particular scheme has not been proposed earlier in any context.

We began with an investigation of the effects of ALC on the steady-state behavior of a simple one-dimensional population dynamics model. As the calculation of the magnitude of ALC involves population size over two generations, the dimensionality of the system is increased, which makes precise analytical results difficult. Therefore, in this study, we limit ourselves to numerical investigations of the effects of ALC. We used the widely-studied Ricker map (Ricker, 1954) to represent the dynamics of the populations. This model is given as $N_{t+1}=N_t \exp(r(1-N_t/K))$ where N_t, r and K denote the population size at time t, per-capita intrinsic growth rate and the carrying capacity respectively. In the absence of any external perturbation, this two-parameter model follows a period-doubling route to chaos with increase in the intrinsic growth rate, r (Fig. 1A; May and Oster, 1976). In Figs. 1 and 2A, we studied the steady-state behavior by iterating the Ricker model in the absence of any noise for 1000 steps (larger number of iterations did not lead to any qualitative changes in the graphs), and plotting the final 100 values. We also computed the fluctuation index (Dey and Joshi, 2006a) of the populations as a measure of the corresponding constancy stability. The fluctuation index (FI) is a dimensionless measure of the average one-step change in population numbers, scaled by the average population size (see Section 3.3.1 for details). As expected, when the population settles to a stable point equilibrium, the FI is zero, but as the population enters the two-point limit-cycle zone, the FI increases (Fig. 1A). However, when the population becomes chaotic, the trajectory visits a large number of points between the upper and lower bound, which can stabilize, increase or even reduce the FI (Fig. 1A). This demonstrates that there need not necessarily be a