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Original Research Article

A graphical method for pre-image population analysis using abundance data series: Implications for management and conservation practices

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ABSTRACT

A graphical method was developed to determine the six landmarks of pre-image population analysis (PPA) (Levins, 2000; Levins et al., 2013), using consecutive time series of abundance data. PPA offers an opportunity to assess the chance that a population exhibits chaotic dynamics, increasing the uncertainty of predictions and/or the success of management interventions. The proposed method was designed for the simplest non-linear difference equation $[x_{n+1} = rx_n(1 - x_n)]$, a prerequisite of which is that the population describes a unimodal shape in the interval map, involving positive/negative self-feedback and a discontinuous breeding (discrete) pattern. Many different mathematical unimodal forms (shapes) and relations among landmarks can be found in the interval map. The unimodal shape was constructed through three segments: the first segment starts at zero on the x_n axis and rises until the peak value; the second segment links the peak with the equilibrium value (~average abundance); the last segment connects the equilibrium and 1.0 on the x_n axis. The method was applied with two (not real) abundance data sets of one species inhabiting different habitats. Using this graphical method, it was analytically possible to determine that a similar man-made intervention could erase or cause chaotic population dynamics, helping identify when and to what extent we can intervene. We propose this method for PPA as a complementary tool, which can aid in single-species management decisions and the adoption of conservation practices.

1. Introduction

Pre-image population analysis (PPA) was developed by Levins (2000) and Levins et al. (2013) to assess the impacts of human intervention strategies on the dynamics of populations that one wants to manage. The principal requirement is that populations describe a unimodal pattern and the method considers those cases in which the dynamics of a population are represented by the following general equation:

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

where x_n is the population abundance at time n, the function $f(x)$ is non-negative, $[f(0) = 0]$ and x_{n+1} is the abundance in the next time period $n + 1$. The unimodal dynamics in the interval map mean that $f(x)$ starts at zero, rises to some peak value and then declines asymptotically towards zero (Fig. 1a), involving positive and negative self-feedbacks (May, 1976; Levins et al., 2013). Therefore, it is possible to find many different mathematical unimodal forms (shapes) for $f(x)$ (Fig. 1a) (Levins, 2007; Levins et al., 2013). PPA is a qualitative-based approach to understanding population dynamics from the shape of the curve $f(x)$. In this case, the curve is related to the following six landmarks: x^* = equilibrium (~average values) (blue line), P (peak) at which $f(x)$ reaches its maximum magnitude (green line), the maximum value, $M = f(P)$, and the minimum value, $m = f(M)$ (both constitute the interval of the permanent region) (red lines), y_{-1} = pre-image 1 $[x^* = f(y_{-1})]$, and y_{-2} = pre-image 2 $[y_{-1} = f(y_{-2})]$ (blue lines) (Fig. 1b). In order to determine graphically y_{-1} and y_{-2}, we start from equilibrium x^*, then a parallel line to x_n axis back to the curve $f(x)$, next a parallel line to x_{n+1} axis to the bisector $x_n = x_{n+1}$, obtaining y_{-1} on x_n axis; then again horizontally back to the curve $f(x)$ next vertical line to bisector obtaining y_{-2} on x_n axis (blue lines). For further detail, see Levins et al. (2013). If y_{-2} lies within the permanent region (that is, if $y_{-2} > m$), the population dynamics are chaotic, satisfying the criterion for the determination of chaos given by Li and Yorke (1975), the sequence of which is $x_3 < x_0 < x_1 < x_2$. Whereas the local stability of an equilibrium value depends on the slope of the intersection between the unimodal shape and the bisector ($x_n = x_{n+1}$), the chaotic properties depend on the relations between the six landmarks and/or the form of the shape; therefore, it is possible to have a shape that gives a locally stable equilibrium and yet is chaotic (Levins, 2007). Fig. 1b shows the

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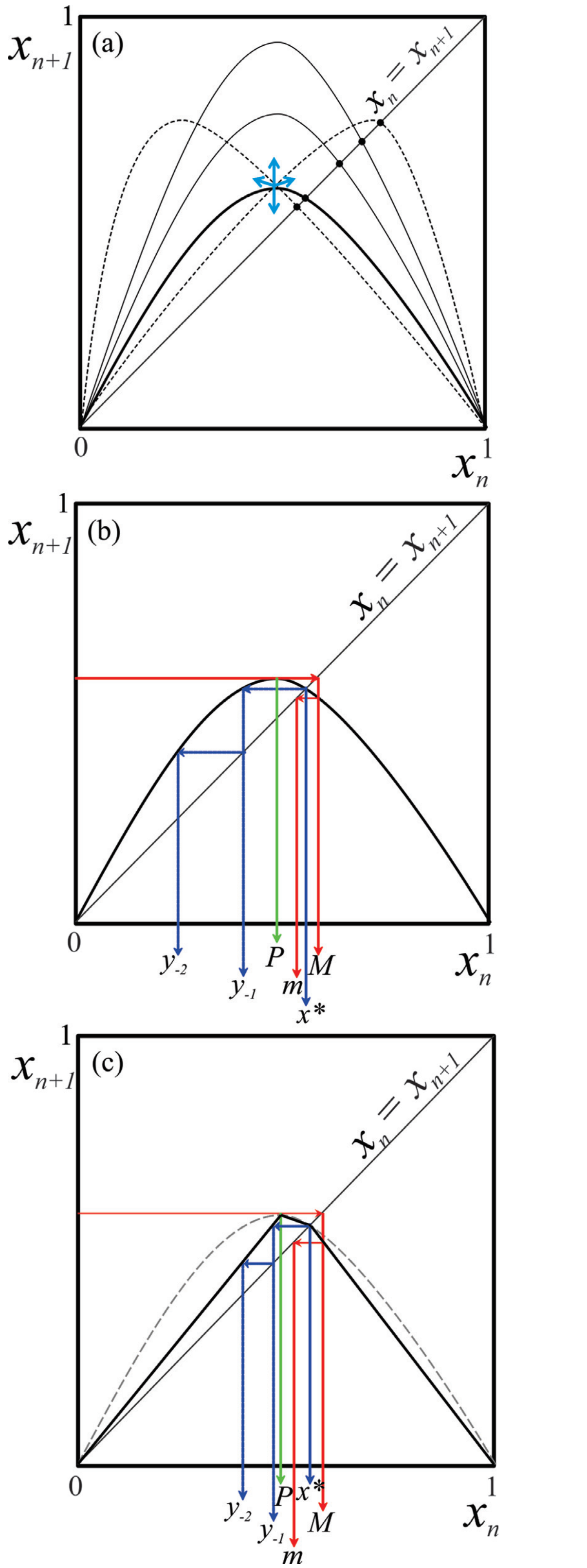

Fig. 1. Web map for population equation of the form $x_{n+1} = f(x_n)$, with the equilibrium line $x_n = x_{n+1}$. (a) The different shape types for the unimodal curve; (b) the six landmarks of pre-image population analysis determined directly using the curve $f(x_n)$; (c) the six landmarks of pre-image population analysis determined using three segments (current proposed method). Note: the hierarchical order of the six landmarks obtained in (b) and (c) is maintained.

six landmarks using the simplest nonlinear difference logistic equation:

$$x_{n+1} = rx_n(1 - x_n), \tag{2}$$

where *r* is the population growth rate and x_n and x_{n+1} are similar to Eq. (1). Eq. (2) requires non-overlapping generations. This prerequisite is achieved as many invertebrate species breed once per year and the whole population size structure is constituted by several cohorts (generations). In spite of this restriction, Eq. (2) could be still used with reasonable agreement between observed and predicted data, as described by Çambel (1993).

Human interventions in natural populations induce changes not only at the population level, but also in the relationships with other species in the community and/or ecosystem (Levins et al., 2013; Ortiz and Levins, 2011, 2017). An intervened population reacts by changing principally its equilibrium values, size/age structure, spatial distribution, growth parameters, reproduction output and local and global stability; it also presents periodic oscillations and even cause or eliminate chaotic dynamics (Levins, 2000; Levins et al., 2013). Although the abundance of any population naturally oscillates around its equilibrium value (average abundance) (Lewontin and Levins, 2007a,b), changes over years (time series of abundance) could offer an opportunity to assess the chance that a population exhibits chaotic dynamics, increasing the uncertainty of predictions and/or the success of management interventions (Levins, 2000). Likewise, if populations are intervened yearly (reduced, exploited and re-stocked), it is possible to evaluate the consequences of past management strategies and how they could be improved in the future.

Chaos refers to a particular class of mathematical phenomena within a subdiscipline of nonlinear dynamical complex systems (Patten, 1997; Levins, 2000). Nevertheless, how common chaos occurs in nature still remains to be determined (Zimmer, 1999; Turchin and Ellner, 2000; Mandal et al., 2006; Lewontin and Levins, 2007c). Different types of chaos can be distinguished, such as regularities in chaotic dynamics, bounds to chaotic trajectories, correlation patterns among chaotic variables that provide prescriptions for detecting chaos-prone or chaos-resistant systems and strategies that suppress or promote chaotic properties (Levins, 2000; Lewontin and Levins, 2007c). Although some authors set chaos in opposition to order (anti-chaos) (Kauffman, 1991; Jørgensen, 1995; Mandal et al., 2006), others consider (theoretically) chaotic fluctuations of dynamical systems to be desirable because they provide an opportunity for control (Mandal et al., 2006) and favour high biodiversity (Huisman and Weissing, 2002; Vandermeer, 2006). Yet others view chaos as beneficial, as in the rhythms of heart, considering regularities a risk factor (Levins, 2000; Peng et al., 2000). Likewise, the dynamic stability of moving equilibriums of complex systems may be steady, transient and even chaotic (Çambel, 1993; Levins, 2000). In this work, we consider that either naturally or as consequence of human intervention, any population could exhibit a bounded non-regular oscillation of abundance (chaotic dynamics), which will increase the uncertainty of future abundance values. Thus, human intervention in a population exhibiting chaotic dynamics could also reduce the bounds or even eliminate chaos.

This paper proposes a simple graphical method for applying pre-image population analysis (PPA) using temporal abundance data series of a species with a discontinuous breeding (discrete) pattern. It is important to note that the abundance series were generated randomly (routine of Excel) and used only for testing the method. Although the data sets do not represent real population dynamics, the range of values created can be easily found in marine benthic species.

2. Methods

Fig. 1b shows a general unimodal shape of *f(x)* in the interval map using Eq. (2). The proposed method for building the shape of *f(x)* is through three segments (straight lines), as shown in Fig. 1c. The first segment starts at zero on the x_n axis and rises until the peak value (*P*);