



Ecological change points: The strength of density dependence and the loss of history

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ABSTRACT

Change points in the dynamics of animal abundances have extensively been recorded in historical time series records. Little attention has been paid to the theoretical dynamic consequences of such change-points. Here we propose a change-point model of stochastic population dynamics. This investigation embodies a shift of attention from the problem of detecting when a change will occur, to another non-trivial puzzle: using ecological theory to understand and predict the post-breakpoint behavior of the population dynamics. The proposed model and the explicit expressions derived here predict and quantify how density dependence modulates the influence of the pre-breakpoint parameters into the post-breakpoint dynamics. Time series transitioning from one stationary distribution to another contain information about where the process was before the change-point, where is it heading and how long it will take to transition, and here this information is explicitly stated. Importantly, our results provide a direct connection of the strength of density dependence with theoretical properties of dynamic systems, such as the concept of resilience. Finally, we illustrate how to harness such information through maximum likelihood estimation for state-space models, and test the model robustness to widely different forms of compensatory dynamics. The model can be used to estimate important quantities in the theory and practice of population recovery.

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1. Introduction

Change more than stasis has perplexed both theoretical and empirical students of ecological time-series. Questions like: “when is a change in dynamics going to occur?”, or “why does a change in dynamics occur?” have preoccupied ecologists working in population dynamics for decades now (Bulmer, 1975). Yet, relatively missing in the theoretical population ecology literature (but see Scheffer, 2009) is an in-depth exploration of how a change in an ecological process, such as density dependence, can drive change in the statistical properties of a (inherently stochastic) dynamic system. How these in turn result in changes with direct management implications is a question of paramount relevance in conservation biology.

The origin of this paper can be traced to a theoretical and empirical study of the population dynamics of a salmonid species by members of the Taper laboratory and colleagues (Staples et al., 2004, 2005, 2006; Muhlfeld et al., 2006; Dennis et al., 2006; Taper et al., 2008; Staples et al., 2009). In particular, we were then

aiming at modeling the reaction of the population dynamics of a Bull Trout population (*Salvelinus confluentus*) to a drastic change in the community composition. Such change was noticeable by eye in the trends of the annual counts of adult females (data from the Montana Fish and Wildlife Service): around 1991, a marked drop in abundances consistently occurred in different tributaries of the affected river and lake system. This scenario led us to specify a natural model candidate: a population dynamics model with a change-point. After all, that very same statistical model had long been used in statistical time series modeling. Managers were and are eager for answers to questions like: how were the dynamics before the change affecting the dynamics after the change, and the extent of the change? After so many years fluctuating at low abundances, is the population expected to recover? If so, how long does the recovery process take?

The strength and effect of density dependence has long been a focus of theoretical and applied population ecology (Holt, 1985; Lebreton and Gimenez, 2013). Although the dependence of the per capita growth rate of a species on its own density or abundance is now widely regarded as a main driver of population dynamics, such proposition still instills rich debates, theoretical problems and practical dilemmas (see citations in Dennis and Taper, 1994;

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Dennis et al., 1998; Freckleton et al., 2006). Our approach directly links a change in dynamics with this central concept in theoretical ecology.

The purpose of this paper is to show that progress in understanding population trends with a change point does not reside per se in the implementation of statistical methodologies aiming at detecting and quantifying change. Rather (through the analysis of these Bull Trout population trends) we found that hidden within the numerical evaluation of the standard matrix model specification of the change-point auto-regressive moving average model, was an ecologically meaningful mechanistic process. Clear patterns and coherent algebraic structures appeared that showed how the strength of density dependence shapes the post change-point dynamics. These expressions partitioned the variance components of the stochastic population process in a way that it allowed us to directly answer those important managerial questions through changes in the strength of density-dependence. Surprisingly then, parameter estimation turned out to be a simple by-product of the process of scientific inquiry of what a stochastic model was really implying.

We strongly believe that the results presented in this paper are generally important for two reasons: first, these results have been all along within the reach of any statistical analysis of population time series data but have so far been overlooked, hidden within the associated matrix algebra calculations of any statistical time series analysis. Second and most importantly, to our knowledge no other work extracts from routine matrix algebra calculations like we do, the explicit and readily interpretable algebraic forms that allow the analyst to go back and forth between the statistical and numerical phrasing of a change and its ecological interpretation.

Statistical time series models with change points in population dynamics have long been used (Bulmer, 1975) but are nowadays rarely routinely considered in ecological analyses despite being extensively studied in the statistical literature (but see Thomson et al., 2010; Packer et al., 2005; Hooten and Wikle, 2007; Andersen et al., 2009; Ives and Dakos, 2012). Asymptotics of maximum likelihood parameter estimates have been derived (Hansen, 1992; Garcia, 1998; Timmer and Pignatiello, 2003; Jandhyala et al., 2013). Hypotheses tests for the presence of change points have been proposed (Picard, 1985; Andrews, 1993; Bai and Perron, 1998; Lavielle and Moulines, 2000; Perreault et al., 2000; Yuan, 2013). Quality control theory features studies of how to incorporate change point warnings in control charts (Perry, 2010; Amiri and Allahyari, 2012; Zhou, 2013). These statistical methods usually test whether an observed time series of population abundances (or densities) depart from a fixed deterministic equilibrium, or from a stochastic stationary distribution. In the first approach, the observed population abundances are observations with measurement error (observation error) added to a deterministic equilibrium or trend. In the second approach, stochastic perturbations are included in the dynamic model to describe the natural fluctuations in abundance. These natural fluctuations are also known as “process noise” (Dennis et al., 2006). With process noise, concepts from deterministic ecological accounts of population regulation take on new forms. For instance, a stable equilibrium of population abundances becomes a stationary probability distribution in stochastic population models (Dennis and Patil, 1984). Although these statistical studies provide substantial underutilized opportunities for ecological data analysis, missing to date is an ecological understanding of the dynamical properties of populations undergoing a change point.

The last twenty years of research in statistical population dynamics concentrated on parameter estimation, model selection and hypothesis testing of models with and without process and observation error (Dennis and Taper, 1994; Zeng et al., 1998; de Valpine and Hastings, 2002; Ives et al., 2003; Clark and Bjørnstad, 2004; Dennis et al., 2006; Lele et al., 2007; Ponciano et

al., 2009; Polansky et al., 2009; Dennis et al., 2010; de Valpine, 2012; Sæther et al., 2013). This research program is warranted because the effective statistical coupling of empirical observations with mathematical models is critical for testing hypotheses concerning population regulation (Lele and Taper, 2011). However, the ecological investigation of populations undergoing change has lagged behind the attention to statistical issues (Dennis et al., 2006; Knape, 2008). This paper seeks to understand what are the ecological consequences of population processes that are not static, but undergo change. To do that, we reveal how the analytical phrasing of a change in a dynamic model translates into readily interpretable and closed-form mathematical changes in the stochastic properties of the population process.

The key idea of this paper is to represent an ecological change point as a saltational change in the parameters of the stochastic population model. Such a change produces both a shift in the stationary distribution of population abundance and a transition to a new equilibrium distribution. We obtain simple formulae characterizing the statistical distribution of the population process during the transition between stationary distributions of abundance. Our study demonstrates that certain historical properties of a population's growth dynamics are determined by the strength of density-dependent processes. In particular, a time series transitioning from one stationary distribution to another contains information about where the process was before, where is it heading, and how long it is going to take to get there. We illustrate how to harness the information in time series containing transitional portions via maximum likelihood estimation for state-space models. The model proposed here provides new insights into the role of density dependence in shifting environments. This model also represents a practical tool for detecting and predicting change events in population monitoring.

2. The strength of density dependence in discrete time models

Consider the general discrete time population growth model $n_{t+1} = f(n_t) = \lambda(n_t)n_t$, where n_t is the population density or abundance at time t and $\lambda(n_t)$ is the (density-dependent) per capita growth rate. Assume that $f(n)$, the recruitment map, is continuously differentiable and that n^* is its non-trivial equilibrium abundance (i.e. its satisfies $f(n^*) = n^*$).

Three measures of the strength of density dependence have been suggested. The first measure is motivated by thinking of the strength of density dependence simply as the marginal effect on the per capita growth rate of an increase in density (Holt, 1985; Holt and Barfield, 2012), which according to our general setting, corresponds to $\partial \lambda(n_t) / \partial n_t$. This is a measure of the effects of density at the individual – not population – level that has been used, among other things, to phrase an evolutionary perspective of intra-specific competition as the way individual, demographic traits respond to an increase in density (Holt and Barfield, 2012). Because for some discrete, density-dependent maps the per capita growth rate $\lambda(n_t)$ is written as an exponential function (as in the Ricker or in the Gompertz equations, see Dennis and Taper, 1994; Lebreton and Gimenez, 2013), the marginal effect of an increase in density can be conveniently measured and plotted in the log-scale of the per capita growth rate by computing $\partial \ln \lambda(n_t) / \partial n_t$.

The second measure corresponds to the derivative of the recruitment map $f(n)$ at equilibrium. Such measure can be directly read from the graph of $f(n)$ as a function of n as the value of the slope when $f(n)$ crosses the 1:1 line. It is important to note that a consideration of both an individual and a population wide measure of density dependence is of obvious importance in population ecology to explain persistence, average abundance, bounds on temporal stability and in general, for a careful understanding of the unfolding of population dynamics (Holt and Barfield, 2012).

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