Changing environments causing time delays in population dynamics

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ABSTRACT

We use a linear diffusion process to approximate a stochastic density regulated population model where parameters can change through time. Contrary to stationary models, there is a difference between the expected value and the carrying capacity of a population at any given time. This time delay can be considerable and depends on the vital rates of the population and the magnitude of the change. We emphasize the importance of acknowledging this difference when assessing viability of populations. As an illustration, we consider the population of Norwegian spring spawning herring and its collapse in the 1960s. Based on our analysis, the stock was already at a critical level a decade before the collapse was observed.

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1. Introduction

Population dynamics is most commonly analyzed by stationary processes, assuming no catastrophic effects or continuous trends in the environment. A major problem in population viability analysis (PVA) is then the exploration of mean time to extinction [1], or derivation of prediction intervals for the time to extinction [2]. These analyzes are important in relation to the precautionary principle [3], that is, how to avoid unacceptable small population sizes [4], and estimating the probability of extinction [5].

However, human activities often affect populations in ways that make the stationary assumption unrealistic. By introducing dynamic parameters that change through time, discrete or continuous changes in the environment, caused by human activities, can be dealt with. Examples of sudden changes are construction of dams for hydro-electrical power production, forest clearance for roads or to acquire land for agriculture [6], and accidents such as oil spills or the release of other pollutants. A recent paper by Fukaya et al. [7] studies the effect of habitat fluctuations on the population dynamics of a marine copepod. Such changes in habitat can be modeled as temporal variation in the growth rate of a species. Gradual changes may occur due to climate change, leading to trends in e.g. temperature and climate indices such as the North Atlantic Oscillation index [8], or changes in stochastic variability. A study on climate effects on Eurasian oystercatcher by van de Pol et al. [9] used a stage-structured model, and showed that the

time to extinction increased as the mean average temperature increased, while an increase in the standard deviation of average temperature reduced the time to extinction. Renwick et al. [10] used generalized linear models to study changes in species abundance under climate change, in addition to other explanatory variables such as land, habitat and rainfall. Under different scenarios for increasing mean global temperature, they predicted an increase in population size for Eurasian nuthatch and green woodpecker, and a decrease in abundance for Eurasian curlew and meadow pipit. Climate effects have also been studied for mammals, e.g. seal [11], red deer [12] and soay sheep [13], and for fish species such as the Atlantic cod [14].

Another anthropogenic effect is overexploitation which has driven many populations extinct, or close to extinction [15–20]. With increasingly effective technology, harvesting has introduced dramatic effects on the population dynamics; effects that may be represented by temporal changes in the parameters describing their dynamics. For instance, the collapse of the Norwegian spring spawning herring population at the end of the 1960s was followed by a period of about 30 years when the population could not be harvested at all [15].

The dynamic response of a given species to changes in the environment, for example caused by the above mentioned human activities, depends in general on how the mean vital rates of survival and fecundity are affected. The dynamics of populations change in different ways depending on which parameters or characteristics of the species that respond to the environmental changes, as well as the values of other parameters. Here, we study such responses, analyzing in particular how changes in population

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dynamics are delayed depending on the biological parameters being affected and the initial dynamics of the populations.

Stationary population fluctuations can often be described, with sufficient accuracy, by three basic quantities; the carrying capacity (usually defined as the population size with zero growth in the average environment), the magnitude of the noise, and the mean return time to equilibrium, which is closely related to the population growth rate at small densities. The mean population size will then be close, or practically equal, to the carrying capacity. Here, we emphasize that analysis of populations in temporally changing environments requires a clear distinction between these concepts. The actual state of a population can now be expressed by two different quantities. The population size itself describes exactly the present status. However, at a given time and environment, the individuals will have some mean vital rates of survival and fecundity, together with effects of density, that determine the expected dynamics of the population, provided that there are no more environmental changes. Under changing environments, there may be a substantial difference between expected population size and carrying capacity, depending in particular on the mean return time to equilibrium. We will analyze this difference in detail, and give simple rules of thumb for how to assess its magnitude. We propose that the precautionary principle should be implemented by analyzing this difference as a major component of the PVA.

Our method will also demonstrate the difference between a pure statistical approach and a population dynamic approach. For example, a common statistical approach is to detrend a time series before fitting an ARMA (p, q) model to the remaining stationary time series [21]. Such approaches do not pay attention to the important distinction between the observed mean population size and the underlying carrying capacity with the implication that the precautionary principle will not be considered with maximum efficiency.

This distinction will be analyzed by linearizing the rather general theta-logistic process on the log scale and approximating it by a continuous time Ornstein–Uhlenbeck process [1]. For stationary models, such linearizations are known to give very accurate descriptions. The simplicity of the Ornstein–Uhlenbeck process makes it possible to model all three parameters; growth, return to equilibrium (or strength of density dependence) and the variance, as general functions of time. The modified process will be a Gaussian process where log population sizes at any time follow a multivariate normal distribution with simple analytical expressions for the parameters. In particular, we derive simple expressions for the changes in mean and variance of log population size. We apply this model to study different types of deterministic environmental changes in dynamic parameters, such as sudden changes and linear trends, and we suggest simple methods for analyzing changes in carrying capacity as an important part of a PVA. Generally, the changes in parameters may also be stochastic, sometimes called parameter drift [22,23], but such changes are outside the scope of this paper.

We first present the purely analytical results for the linear process. Next, we discuss how the parameters in the linear process relate to parameters in stochastic density regulated population processes with environmental noise. Finally, we present some examples on sudden and linear changes in biological parameters, with special emphasis on time delays and the difference between expected population size and carrying capacity.

2. Methods

2.1. Linear diffusion process

Consider the linear diffusion process for log population size X_t at time t with infinitesimal mean $\alpha(t) - \beta(t)X_t$ and infinitesimal variance $\sigma^2(t)$ [24],

$$dX_t = [\alpha(t) - \beta(t)X_t]dt + \sigma(t)dB_t \quad (1)$$

where B_t is standard Brownian motion with expectation zero and unit variance [1] such that $E[dB_t] = 0$ and $Var[dB_t] = dt$. The diffusion parameters α, β and σ^2, are general functions of time. Defining $\Upsilon(s, t) = \exp(\int_s^t \beta(v)dv)$ for any $0 \leqslant s \leqslant t$, the solution to this linear stochastic differential Eq. (1), derived in Appendix A, is

$$X_t = \Upsilon^{-1}(0, t)\left[X_0 + \int_0^t \Upsilon(0, u)\alpha(u)du + \int_0^t \Upsilon(0, u)\sigma(u)dB_u\right],$$

where $\Upsilon^{-1}(s, t) = \exp(- \int_s^t \beta(v)dv)$. Assuming $X_0 \sim N(\mu_0, v_0)$, the log population sizes at any set of times follow a multinormal distribution with expectation

$$E[X_t] = \Upsilon^{-1}(0, t)\left[\mu_0 + \int_0^t \Upsilon(0, u)\alpha(u)du\right] \quad (2)$$

and covariances

$$.Cov[X_s, X_t] = \Upsilon^{-1}(s, t)\Upsilon^{-2}(0, s)\left[v_0 + \int_0^s \Upsilon^2(0, u)\sigma^2(u)du\right]. \quad (3)$$

2.2. Mean and variance

Taking the expectation of $X_{t+dt} = X_t + dX_t$ and writing $\mu_t = E[X_t]$, we get (see Appendix A.1)

$$\frac{d\mu_t}{dt} = \alpha(t) - \beta(t)\mu_t. \quad (4)$$

The solution to this first order differential equation is Eq. (2). Moreover, for $\beta(t) > 0$ and $k_t = \alpha(t)/\beta(t)$, Eq. (4) gives the difference between expected log population size and the carrying capacity on the log scale

$$k_t = \mu_t + \frac{1}{\beta(t)}\frac{d\mu_t}{dt}. \quad (5)$$

We see that $k_t = \mu_t$ when $d\mu_t/dt = 0$, while the carrying capacity on the log scale is smaller than expected log population size for decreasing expectations. The difference is large for small values of $\beta(t)$, corresponding to large mean return times to equilibrium.

Similarly, for the variance $v_t = Var[X_t]$ we get the first order differential equation

$$\frac{dv_t}{dt} = -2\beta(t)v_t + \sigma^2(t) \quad (6)$$

with solution given by Eq. (3) (for $s = t$). Again, for $\beta(t) > 0$ for any t, Eq. (6) can be written as

$$\tau_t^2 = \frac{\sigma^2(t)}{2\beta(t)} = v_t + \frac{1}{2\beta(t)}\frac{dv_t}{dt} \quad (7)$$

where τ_t^2 is the stationary variance of X_t under constant vital rates, determined by the environmental conditions at time t.

The process with constant parameters is the well known Ornstein–Uhlenbeck process [1]. With initial value X_0, X_t then has a normal distribution with expectation

$$E[X_t] = \frac{\alpha}{\beta} + \left(X_0 - \frac{\alpha}{\beta}\right)e^{-\beta t}$$

and variance

$$Var[X_t] = \frac{\sigma^2}{2\beta}\left(1 - e^{-2\beta t}\right),$$

which are special cases of Eqs. (2) and (3). Thus, in the limit as $t \to \infty$, the process has a normal stationary distribution with mean α/β and variance $\sigma^2/(2\beta)$ [1]. If the parameters are functions of time for $t \leqslant t_0$, but kept constant after t_0, then the process is the above Ornstein–Uhlenbeck process for $t > t_0$.