



Delay driven spatiotemporal chaos in single species population dynamics models



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ABSTRACT

Questions surrounding the prevalence of complex population dynamics form one of the central themes in ecology. Limit cycles and spatiotemporal chaos are examples that have been widely recognised theoretically, although their importance and applicability to natural populations remains debatable. The ecological processes underlying such dynamics are thought to be numerous, though there seems to be consent as to delayed density dependence being one of the main driving forces. Indeed, time delay is a common feature of many ecological systems and can significantly influence population dynamics. In general, time delays may arise from inter- and intra-specific trophic interactions or population structure, however in the context of single species populations they are linked to more intrinsic biological phenomena such as gestation or resource regeneration. In this paper, we consider theoretically the spatiotemporal dynamics of a single species population using two different mathematical formulations. Firstly, we revisit the diffusive logistic equation in which the per capita growth is a function of some specified delayed argument. We then modify the model by incorporating a spatial convolution which results in a biologically more viable integro-differential model. Using the combination of analytical and numerical techniques, we investigate the effect of time delay on pattern formation. In particular, we show that for sufficiently large values of time delay the system's dynamics are indicative to spatiotemporal chaos. The chaotic dynamics arising in the wake of a travelling population front can be preceded by either a plateau corresponding to dynamical stabilisation of the unstable equilibrium or by periodic oscillations.

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1. Introduction

Factors and mechanisms determining the spatial population distribution of ecological species are a major focus of interest in ecology (Fortin and Dale, 2005; Ritchie, 2010). Often the distribution shows remarkable spatial variability, which is usually referred to as patchiness (Levin, 1994; Rietkerk et al., 2004), where areas or 'patches' of high population density are separated from areas where the given species is either present at a very low density or is absent altogether. A classical example of such a patchy spatial distribution is given by plankton (Levin and Segel, 1976; Martin, 2003), although terrestrial species, in particular insects, often exhibit considerable spatial variability as well (Liebhold et al., 2013).

One obvious explanation of this phenomenon is swarming behaviour (Okubo, 1986), especially when it is reinforced by social

interactions between the animals (e.g. Mogilner and Edelstein-Keshet, 1999; Mogilner et al., 2003) and/or by taxis (Tyutyunov et al., 2004, 2009). On a larger spatial scale, an intuitive explanation of the spatial heterogeneity in species distribution lies in environmental variability, e.g. spatial distribution is being driven by the heterogeneous distribution of resources (Liebhold et al., 1994; Grünbaum, 2012). However, in many cases this does not seem to be the case as the observed population distributions appear to be largely uncorrelated with the environment (Powell et al., 1975; Sharov et al., 1997). The heterogeneous spatial population distribution can also arise as a result of biotic interactions. In particular, there is a large body of literature showing, both theoretically and empirically, that a spatial pattern can be a result of predator–prey or host–parasite interactions (Hassell et al., 1991; Hastings et al., 1997; Davis et al., 1998; Petrovskii and Malchow, 1999; Jankovic and Petrovskii, 2013), or multi-specific competition (Petrovskii et al., 2001; Adamson and Morozov, 2012; Mimura and Tohma, 2014). Note that, in the case of biotic-driven pattern formation, the patterns can be regarded as self-organised, i.e. they are not related

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to any external forcing; in fact, they can arise in a uniform environment.

Self-organised pattern formation is often related to instability of the spatially uniform distribution; a well-known example is given by the Turing instability (Segel and Jackson, 1972; Klausmeier, 1999). A necessary condition of the Turing instability is the differing diffusivity of interacting species; in order to make the instability practically observable (i.e. to occur in a reasonably broad range of population dynamics' parameters), the diffusion coefficients have to be at least an order of magnitude apart. This large difference in the mobility of a prey and its predator does not often happen, and hence the ecological importance of the Turing scenario of pattern formation is rather limited (but see Sherratt, 2013).

An alternative mechanism is sometimes referred to as biological turbulence¹ or a “wave of chaos” (Petrovskii and Malchow, 2001) which becomes possible when the dynamics of the interacting species are oscillatory. From a theoretical perspective, this is usually related to the existence of a stable limit cycle, e.g. see Turchin (2003). The properties of the population's spatial distribution emerging due to this mechanism were shown to be in agreement with field observations (Medvinsky et al., 2002; Petrovskii et al., 2003; Malchow et al., 2008). However, the capacity of biological turbulence to explain patchiness of ecological populations is somewhat limited too, as the existence of the limit-cycle population oscillations requires interaction of the given species (prey) with its specialist predator (cf. Rosenzweig, 1971; May, 1972). Specialist predators are relatively rare in nature and that may explain why genuine predator-prey cycles are not often seen.² As long as the predator is a generalist, in a realistic multi-species community predator-prey cycles are unlikely to occur, as the changes in the density of prey become uncoupled from that of the predator because of the complicated switching behaviour of the latter (Comins and Hassell, 1976; Holt, 1983; Morozov and Petrovskii, 2013; Van Leeuwen et al., 2013). Heterogeneous population distribution is therefore a far more general phenomenon than the theoretical mechanisms that have by far been brought forward as its explanation.

There is, however, another feature of population dynamics as ubiquitous as species heterogeneity, and this is time delay. Delayed density dependence is thought to be one of the main factors causing population fluctuations (Berryman and Turchin, 1997). The most commonly considered causal mechanisms are resource competition (Hansen et al., 1998), cannibalism (Briggs et al., 2000), and maternal effects (Ginzburg and Taneyhill, 1994) where the nutritional environment of the parental generation can influence the growth and reproductive potential of the next generation. Delays may also occur as a consequence of developmental time and/or interaction between individuals of different stages (Royama, 1981; Hastings, 1984). In mathematical terms, the destabilisation of a positive steady state, both in nonspatial and spatial systems, usually occurs through the Hopf bifurcation (Green and Stech, 1981; Fowler, 1982; Busenberg and Huang, 1996; Li et al., 2008; Su et al., 2009) that leads to limit-cycle oscillatory behaviour. We mention here that such destabilisation does not always happen; in particular, if the population growth is damped by a strong Allee effect, an increase in time delay does not necessarily lead to the Hopf bifurcation, e.g. see Jankovic and Petrovskii (2014).

¹ The term “biological turbulence” was suggested to Sergei Petrovskii by Lutz Schimansky-Geier in a private discussion in 1999.

² The famous hare-lynx cycle (Elton and Nicholson, 1942; May, 1975) is sometimes regarded as the only available example, although there are different opinions on that (cf. Sherratt and Smith, 2008) and the discussion is by no means over.

In this paper, we examine the inherent relation between these two phenomena, i.e. time delays and pattern formation. We are especially interested in the possibility of the onset of spatiotemporal chaos and, respectively, the formation of irregular spatial patterns. We mention here that, whilst the dynamics of time-delayed non-spatial systems are understood relatively well, time-delayed spatial systems pose a much bigger challenge. Although there is a large body of literature concerned with time-delayed spatially explicit population dynamics (e.g. see the references above), the vast majority of it is concerned with either a travelling front or a periodic pattern (Ashwin et al., 2002; Yoshida, 1982; Su et al., 2009). Meanwhile, in population systems where limit cycles appear for other reasons (i.e. not related to time delay), travelling waves and periodic patterns are known to be only a part of the rich spectrum of spatiotemporal dynamics (Petrovskii and Malchow, 2000) that, in particular, may exhibit chaotic oscillations (Sherratt et al., 1995; Sherratt, 2001; Petrovskii et al., 2001). Correspondingly, the possibility of spatiotemporal pattern formation and chaos in a single species population with time delay is our main interest here. We first consider pattern formation triggered by travelling population fronts in a heuristic delayed diffusion-reaction equation where the delay is included into the per capita growth, and reveal the onset of spatiotemporal chaos in the wake of the front. We then consider a somewhat more realistic model where the delay is appropriately spatially averaged (Britton, 1990; Gourley and Bartuccelli, 1995; Gourley and Chaplain, 2002; Ashwin et al., 2002), which results in an integro-differential model, and show that it exhibits qualitatively similar properties such as, in particular, the onset of chaos.

The remainder of the paper is organised as follows. In the following section (Section 2) we introduce our modelling framework and revisit known analytical results for the stability condition and loss of monotonicity conditions for both Hutchinson's equation and the diffusive logistic equation. We then investigate through numerical simulations the effect time delay has on the diffusive logistic model (Section 3). In Section 4, we introduce a modified model and discuss the concept and reasoning behind the spatial averaging, as well as presenting numerical results. Section 5 summarises our findings.

2. Modelling framework and some analytical results

Temporal dynamics of a single species population can be described by the following generic ordinary differential equation:

$$\frac{dU}{dt} = Uf(U), \quad (2.1)$$

where U is the population size (density) and $f(U)$ describes the per capita growth. For many populations the observed biological reality imposes a saturation level, known as the carrying capacity, which forms a numerical upper bound on growth. Correspondingly, the simplest form of such, the Verhulst-Pearl logistic equation is frequently used to model self-limiting populations:

$$\frac{dU}{dt} = rU \left(1 - \frac{U}{K} \right), \quad (2.2)$$

where r is the intrinsic rate of growth and K is the carrying capacity. Logistic growth implies rapid initial growth at low population densities and a nearly exponential decay to the population's carrying capacity due to the negative feedback through intraspecific competition. Admittedly a simple model, such behaviour is in qualitative agreement with observed dynamics of many populations, especially under laboratory, resource-limited,

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