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Pattern formation in Malthusian growth with transport memory

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Abstract

We consider the effect of memory-dependent transport on the survivability of a population dispersing in a closed domain surrounded by a hostile environment. The model we use combines memory-dependent diffusion with Malthusian growth. The former introduces an additional parameter, the correlation time for memory effects, that must be taken into account in determining the critical length below which survival does not occur. Results are obtained for all possible parametric conditions, and the relevance to non-linear growth conditions is discussed.

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1. Introduction

Fisher's equation [1] describes the dispersal of a growing population through a superposition of simple diffusive motion and logistic growth. The resulting equation, non-linear due to the logistic self-regulation term, has been the subject of considerable interest and study and applied in a wide variety of contexts [1–3]. When the growth is Malthusian, the resulting linear equation provides the basis for obtaining exact analytical results that, with the proper interpretation, describe important aspects of the non-linear problem with logistic growth. Important examples are the minimum wave speed of a travelling wave in an unbounded domain [4], and the critical length below which the population does not survive in a bounded domain [5]. We will be concerned with the latter property here in the context of a model proposed earlier [6] to investigate the effects of transport memory on the properties of travelling wave solutions. An alternative approach to introducing non-local (in time) diffusive effects with application to the identical problem has also been recently considered [7].

Simple diffusion is a long-time limit of a transport process that may have a spectrum of scattering frequencies and a finite signal speed. The latter can be modelled by replacing the local diffusion operator by a non-local operator that includes a memory function with a

correlation time that characterizes the transition to diffusive motion [8]. When the memory function is exponential [6], as we also consider here, the equation for dispersal without growth is equivalent to the telegrapher's equation which has frequently been used as a model for dispersal [9–11].

In [6] the non-linear Fisher equation with the transport term modified to include memory effects was studied relative to the possible speeds for travelling wave solutions. The introduction of a correlation time characterizing the memory effects led to a variety of possible outcomes depending on the interplay of the system parameters; similar results were also obtained in [7]. In this paper we consider the impact of memory effects in determining the critical length below which the population cannot survive. To do this we make use of the analytically tractable Malthusian growth model. For the case of simple diffusion, i.e. when the memory function is a delta function (zero correlation time), this is known as the KISS length [12, 13], and it separates domains in which the population does not survive from those in which growth continues without bound (i.e. it is a bifurcation point). It can be shown [5] that when growth is logistic this length remains the same but when the domain size exceeds this the self-regulation imposed by the non-linear logistic term leads to a patterned steady state. This can be proved rigorously [14, 15] for the case of simple diffusion, but the proof is based on properties of partial differential equations that cannot be applied here since we are considering an integro-differential equation. Here, it seems reasonable to conjecture that logistic self-regulation would also result in a steady state above the KISS length. Therefore, the significance of the results obtained here should be to describe the parameter space dividing survival from non-survival. We will show that the addition of the correlation time as a parameter again leads to a greater variety of possible outcomes than can occur for simple diffusion.

In the next section we obtain a general equation describing the Fourier coefficients of the population density satisfying the memory-dependent evolution equation introduced in [6] for the case of a bounded domain surrounded by a hostile environment. The behaviour of these coefficients depends on the relative magnitudes of the system parameters as well as the Fourier index. We consider the special case where the inverse correlation time is equal to the intrinsic growth rate in section 3 and in section 4 we then consider the more general case where these differ. The results found are discussed in section 5.

2. Analysis

Our starting point is the following equation describing the dispersal of a population having density $n(x, t)$ in the domain $0 \leq x \leq L$ surrounded by a hostile environment so that $n(0, t) = n(L, t) = 0$:

$$n_t = Da \int_0^t dt' e^{-a(t-t')} n_{xx}(x, t') + rn(x, t). \quad (1)$$

The parameters are r the intrinsic growth rate, D the diffusion coefficient and a the inverse correlation time. In the limit $a^{-1} \rightarrow 0$ the transport term reduces to that for simple diffusion. Equation (1) is equivalent to a telegrapher's equation; this follows from differentiation with respect to the time variable and substitution into the resulting equation for the integral term. We comment on this further later, but proceed here by considering equation (1) directly.

If we expand n in the Fourier sine series we can obtain an equation for the coefficients $A_n(t)$ directly from equation (1); for now we assume that as for the case of simple diffusion we only need to consider A_1 but we may note that if $n(x, 0) = n_0 \sin(\pi x/L)$ then $A_n = 0$ for

$n > 1$. Introducing Laplace transforms, which we denote with the transform variable s in the argument, e.g., $A_n(s)$, then from equation (1) it follows that

$$A_n(s) = \frac{(s + a)}{s(s + a) + K_n - r(s + a)} A_{no} \tag{2}$$

where $K_n = (n\pi/L)^2 Da$, $A_{no} = A_n(t = 0)$. If the memory function were a delta function we could neglect s compared to a and

$$A_n(s) \approx \frac{A_{no}}{(s + K_n^* - r)} \Rightarrow A_n(t) = \exp -t(K_n^* - r) \tag{3}$$

where $K_n^* = a^{-1}K_n$, and the critical length L^* follows from $K_n^* = r$ with $n(x, t) \rightarrow 0$ for $L < L^*$ and $n(x, t) \rightarrow \infty$ for $L > L^*$ as $t \rightarrow \infty$. For finite a equation (2) requires consideration of a wider range of interplay among the parameters.

3. Case I: $r = a$

When $r = a$ and $K_1 > a^2$ we have

$$A_1(s) = \frac{(s + a)A_{1o}}{s^2 + (K_1 - a^2)} \tag{4a}$$

so that

$$A_1(t) = A_{1o}[\cos(K_1 - a^2)^{1/2}t + a(K_1 - a^2)^{-1/2} \sin(K_1 - a^2)^{1/2}t] \tag{4b}$$

which becomes negative for values of t for which $[K_1 - a^2]^{1/2}t$ is in the third quadrant; the population does not survive. For $r = a$, $K_1 < a^2$ we find

$$A_1(t) = A_{1o}[\cosh(a^2 - K_1)^{1/2}t + a(a^2 - K_1)^{-1/2} \sinh(a^2 - K_1)^{1/2}t] \tag{5}$$

which grows without bound. Similarly, if $K_1 = a^2 = r^2$ then $A_1(t) = A_{1o}[1 + at]$ and again grows without bound (but much slower). For initial conditions such that some of the $A_n \neq 0$ for $n > 1$, e.g., a delta function at $x = L/2$, then for some value of $n > 1$, $K_n > a^2$. Comparing equations (4) and (5) we see that in this case the growth terms will dominate and the above conclusion remains valid. The previous result for $K_1 > a^2$ also follows for arbitrary initial condition.

4. Case II: $r \neq a$

To begin we look at the special sub-case where $K_1 = ra$ so that

$$A_1(s) = \frac{(s + a)A_{1o}}{s[s + (a - r)]} \tag{6a}$$

leading to

$$A_1(t) = A_{1o} \left[\exp -(a - r)t + \frac{a}{(a - r)}(1 - \exp -(a - r)t) \right]. \tag{6b}$$

If $r > a$ this grows without bound but if $r < a$ we have a non-trivial steady-state limiting solution. When $K_1 \neq ra$ we have

$$A_1(s) = \frac{(s + a)A_{1o}}{s^2 + s(a - r) + (K_1 - ra)} = \frac{(s + a)A_{1o}}{(s - s_1)(s - s_2)} \tag{7}$$

with

$$s_{1,2} = \frac{1}{2}[(r - a) \pm \sqrt{(r - a)^2 - 4(K_1 - ra)}]. \tag{8}$$

Consider first $ra > K_1$ with $r > a$ so that $s_1 > 0$, $s_2 < 0$ and both are real. Then

$$A_1(t) = \frac{A_{1o}[(s_1 + a) \exp s_1 t - (s_2 + a) \exp s_2 t]}{(s_1 - s_2)} \quad (9)$$

which grows without bound. When $r < a$, $ra > K_1$ there are again two real roots with $s_1 > 0$, $s_2 < 0$ and the above conclusions again follow (s_1 and s_2 differ in each case, but this does not affect the qualitative result).

When $ra < K_1$ we first re-write equation (8) as

$$s_1, s_2 = \frac{1}{2}[(r - a) \pm \sqrt{(r + a)^2 - 4K_1}] \quad (10)$$

and distinguish between $(r + a)^2 > 4K_1$ and $(r + a)^2 < 4K_1$. In the former case, when $r > a$, $s_1 > s_2 > 0$ so that $A_1(t)$ is again given by equation (9) and grows without bound. Also, when $r < a$ then $s_1 < s_2 < 0$ and the population does not survive, i.e. $A_1(t)$ will decay to zero. The remaining possibility is for $(r + a)^2 < 4K_1$ in which case $s_1 = \frac{1}{2}[(r - a) + i\sigma]$, $s_2 = \bar{s}_1$, where $\sigma = \sqrt{4K_1 - (r + a)^2}$ and the overbar denotes complex conjugate. From equation (7) it then follows that

$$A_1(s) = \frac{(s + a)A_{1o}}{[s - (r - a)^2/2 + \sigma^2/4]} \quad (11)$$

and

$$A_1(t) = A_{1o} \exp(r - a) \frac{t}{2} \left[\cos \frac{\sigma t}{2} + \frac{(a + r)}{\sigma} \sin \frac{\sigma t}{2} \right]. \quad (12)$$

Regardless of whether r is greater or less than a this becomes negative for $\sigma t/2$ in the third quadrant indicating the population does not survive.

5. Discussion

The above results indicate that memory effects can have a profound influence on the survivability conditions for a population that is undergoing Malthusian growth in a bounded domain surrounded by a hostile environment. When the correlation time is equal to the birth rate (section 3) the critical length is equal to that for simple diffusion but $L = L^*$ does not provide a steady state here. The conditions for a steady state are $K_1 = ra$ with $r < a$. This is an exact result for $n(x, 0) = n_o \sin(\pi x/L)$. For more general initial conditions we cannot rigorously prove that the higher Fourier coefficients will alter this conclusion since the classical Sturm–Liouville theory [16] does not apply here. However, this result is moderately robust since for $K_1 = ra$ we will have $K_n > ra$ and we have shown that when $(r + a)^2 > 4K_n$ or $(r + a)^2 < 4K_n$ and $r < a$ that the A_n will decay. The critical length here is the same as for simple diffusion, but the steady-state population density is greater by a factor $\frac{a}{a-r}$ due to the fact that transport to the hostile boundaries is retarded allowing additional births to occur. This interpretation is consistent with the travelling wave analysis of [6]. This difference is not immediately apparent if instead of equation (1) we had considered the telegrapher's equation derived from it [cf equation (3) of [6]]

$$n_{tt} + (a - r)n_t = Da n_{xx} + arn \quad (13)$$

and naively looked for steady-state solutions by setting the left side equal to zero. Since the resulting equation is identical to that for simple diffusion it might be intuited that the steady-state density also remains unchanged. But that solution requires that the full time-dependent equation (5) be taken into account and, it is easily seen that when n is again written as a Fourier sine series, the Laplace transform of equation (13) with equation (1) leads to equation (2) and the results obtained above.

In summary, we have considered population dispersal in a bounded domain surrounded by a hostile environment as a superposition of memory-dependent transport and Malthusian growth. This introduces another parameter, a , the inverse correlation time, that must be taken into account in determining the conditions for which the population grows, dies or reaches a steady state. We conjecture that, as for simple diffusion, when growth self-regulation occurs, as through the addition of a non-linear logistic term, the conditions for which we found growth will correspond to those for which a steady state is attained. These are for $K_1 \leq ra$ and $K_1 > ra$ with $(r + a)^2 > 4K_1$, $r > a$. However, we would expect that when memory effects do occur $r < a$ will be most likely since $a \rightarrow \infty$ corresponds to simple diffusion.

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