THE STABLE SIZE DISTRIBUTION: AN EXAMPLE IN STRUCTURED POPULATION DYNAMICS.

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1. INTRODUCTION

If some characteristic of the individuals is essential for describing the dynamics of a population properly, one has to distinguish the individuals from each other according to this characteristic. As an example of such a trait, which can take a continuum of values, we shall consider "size" (denoted by the symbol x), by which we mean any relevant quantity satisfying a physical conservation law. *)

Then, to begin with, one has to specify the dynamics of the individuals. The basic processes fall into two categories:

I *Change:* the size of each individual changes continuously (according to some law which has to be specified) when nothing special happens:
$\frac{dx}{dt} = g$ = growth rate = prescribed function of x and, possibly, other variables.

II *Chance:* some individuals undergo spectacular processes, while others do not. One has to specify the chances (per unit of time) that this will happen as a function of x and .... For example,
$\mu = \mu(x) = \mu(x,\dots)$ = chance to die as a function of x,...,
$b = b(x) = b(x,\dots)$ = chance to split into two identical parts as a function of x,... .

(Although we use the word "chance", we shall deal with deterministic models which are based on the assumption of large numbers).

In the second step, one introduces a *density function* n to describe the state of the population and one derives an equation for n by drawing up the *balance* of I and II. For a species which reproduces by binary fission one obtains:

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*) e.g., weight, N-, or P- content, but not age, since there is no conservation of age in the fission process.

$$(1) \qquad \underbrace{\frac{\partial n}{\partial t} + \frac{\partial}{\partial x}(gn)}_{\text{growth}} = \underbrace{-\,\mu(x)n(t,x)}_{\text{death}} \; \underbrace{-\,b(x)n(t,x)}_{\substack{\text{reproduction}\\ \text{sink}}} \; \underbrace{+\,4b(2x)n(t,2x)}_{\substack{\text{reproduction}\\ \text{source}}} ,$$

where $\int_{x_1}^{x_2} n(t,\xi)d\xi$ = number of individuals with size between x_1 and x_2 at time t. (Exercise: explain the factor 4. Hint: check conservation of mass during fission). This is a special case of Sinko & Streifer's (1971) mathematical model for organisms reproducing by fission.

The year 1967 showed a remarkable outburst of papers formulating similar models for the dynamics of structured populations: Bell & Anderson (1967), Fredrickson, Ramkrishna & Tsuchiya (1967), Sinko & Streifer (1967). Although there has been some follow up (see, for instance, Streifer (1974), Oster (1977), Nisbet (this volume) and the references therein), we can conclude today, fifteen years later, that the mathematical theory is still in its infancy (possibly with the exception of age-dependent population growth).

From a mathematical point of view, the theory is concerned with first order partial differential equations with non-local terms (transformed arguments, integrals,...) which are nonlinear as soon as interaction is taken into account. From a biological point of view, the aim is to use information about the behaviour and the physiology of individuals to describe, understand and predict the dynamics of the population as a whole (see Streifer's (1974) excellent survey paper for an elaborate presentation of the main ideas). In practice one frequently encounters the inverse problem: how to use measurements of the density function to derive conclusions about the dynamics of individuals (see, e.g., Bell & Anderson, 1967).

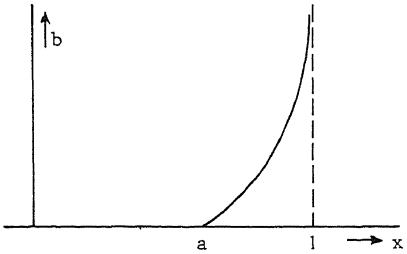
The above observations form the basis for a recently started research project in the Netherlands (at the Mathematical Centre), which aims at analysing specific examples in this category of equations and models with an eye for a general theory. This note is a progress report, based on work of T. Aldenberg, H.J.A.M. Heijmans, H.A. Lauwerier, J.A.J. Metz, H. Thieme (Heidelberg), and the author. We shall deal with two topics:

i) linear equations: convergence towards a stable distribution,

ii) nonlinear equations: interaction via the growth function (a feedback mechanism which admits a clear biological interpretation).

2. THE STABLE SIZE DISTRIBUTION

In this section we assume that g, μ and b are functions of x only. As a further specification of the model we require:



for some $a \in (0,1)$:

$b(x) = 0$, for $x \in (0,a)$

$b(x) > 0$, for $x \in (a,1)$, b continuous,

$\lim_{x \uparrow 1} \int_a^x b(\xi)d\xi = +\infty$.

These are mathematical counterparts of the following biological assumptions:

i) there is a minimal size, called a, which an organism should have in order to have some chance to undergo fission.

ii) there is a maximum size, normalized to be 1, which an organism can reach (note that the chance to grow from a to x without splitting is given by

$$\exp - \int_{T(a)}^{T(x)} b(\xi(t))dt = \exp - \int_a^x \frac{b(\xi)}{g(\xi)}\, d\xi,$$

in case μ equals zero; here $T(x)$ denotes clock time when the organism has size x and $\xi(t)$ the size as a function of time).

On account of i) we supplement (1) with the boundary condition

$$(2) \qquad n(t,\tfrac{1}{2}a) = 0$$

which expresses that organisms with size less than $\frac{1}{2}a$ do not exist. In (1) we interpret the term $4b(2x)n(t,2x)$ as zero for $x > \frac{1}{2}$. The functions μ and g are assumed to be continuous functions on $[\frac{1}{2}a,1]$, with μ nonnegative and g strictly positive. Finally, we assume that the situation at $t = 0$ is known:

$$(3) \qquad n(0,x) = \phi(x), \quad x \in [\tfrac{1}{2}a,1], \quad \phi \geq 0.$$

Question (by analogy with Lotka's celebrated result for unlimited age dependent population growth).

Is it true that

$$(4) \qquad n(t,x,\phi) \sim C(\phi)e^{\lambda_0 t} n_0(x), \quad t \to +\infty,$$

where λ_0 is a real number (the Malthusian parameter or intrinsic rate of natural increase) and $n_0(x) \geq 0$ is a stable size distribution?

Answer yes if $g(2x) < 2g(x)$ (or $g(2x)>2g(x)$),
no if $g(2x) = 2g(x)$.

Elucidation: Consider two organisms A and B with equal size. A splits into a and a. During some time interval a, a and B grow. Then B splits into b and b. How do the sizes of a and b compare? If $g(2x) = 2g(x)$ they are identical and the initial condition is, apart from multiplication, copied again and again. This merry-go-round character implies that all properties of the initial condition remain manifest for all times. In sharp contrast, when $g(2x) < 2g(x)$, only a one-dimensional projection (the constant C) of the initial condition influences the asymptotic behaviour.

We refer to Diekmann, Heijmans & Thieme (in preparation) for a precise mathematical formulation and a proof (in addition this paper will contain extensions to periodic environments, like in Thieme (preprint 1982)). The following *mathematical techniques* are used:

i) eigenvalue problem ⇒ integral operator equation ⇒ positive operator theory ⇒ dominant eigenvalue (Heijmans, preprint 1982).
ii) evolution equation ⇒ integral operator equation ⇒ existence and uniqueness of a solution ⇒ definition of a semigroup.
iii) semigroup + compactness + dominant eigenvalue ⇒ asymptotic behaviour for $t \to +\infty$ (it is remarkable that the condition on g is used only to get compactness of the semigroup after finite time).

Moreover, it is possible to derive a transcendental equation for λ_0 (and the other eigenvalues; Heijmans (preprint 1982)), which in the case $a \geq \frac{1}{2}$ takes the form

$$2 \int_a^1 \frac{b(\xi)}{g(\xi)} \exp\left(- \int_{\frac{1}{2}\xi}^{\xi} \frac{b(\eta)+\mu(\eta)+\lambda}{g(\eta)}\, d\eta\right) d\xi = 1.$$

Here the left hand side with $\lambda = 0$ has the usual interpretation: it is the offspring of the average individual (with $x=a$ taken as the reference point). Similarly, n_0 and $C(\phi)$ are quite computable. So, although the proof uses abstract machinery, the outcome is rather concrete.

3. THE LIMITED WORLD

How does a population of, say, unicellular organisms, react upon a given, limited, supply of nutrients? This question immediately leads to another one: how do the organisms use nutrients for growth and reproduction? The main advantage of structured models is that one can use submodels for processes within the individuals and combine these to obtain an overall population model (Streifer, 1974).

Sinko and Streifer (1971) made a detailed model for a population of the planarian worm Dugesia tigrina, starting from the assumption that the important physiological characteristics can be described by their mass alone. They specified how the available food was distributed among the individuals, how the consumed food was used for maintenance and growth and how the "birth" function was influenced by food shortage. Moreover, they solved the resulting equations numerically and compared the outcome with available data.

In addition to the detailed modelling of real populations, one can try to enlarge understanding and intuition by analysing relatively simple idealized mathematical models. That is the approach taken here.

So assume that g = g(x,c) and b = b(x,c), where c describes the concentration of some important chemical substance. In a chemostat we would have

$$\text{(5)}\qquad \frac{dc}{dt} = \underbrace{\gamma}_{\text{inflow}} - \underbrace{\int_{\frac{1}{2}a}^{1} h(x,c)n(t,x)dx}_{\text{uptake by the population}} - \underbrace{\mu c}_{\text{outflow}}$$

for some function h. (If we are dealing with a structural chemical, as is assumed below, we may set h equal to αg, for some constant α).

Questions: 1) Do we still obtain a stable size distribution?

2) If so, how does the time-dependent factor (the amplitude) behave?

We don't know (yet) the answers in general. However, in the very special case that (abusing notation)

$$\text{(6)}\qquad \begin{cases} \text{i)}\quad b(x,c) = g(x,c)b(x), \\ \text{ii)}\quad g(x,c) = \beta(c)\,g(x), \qquad g(2x) < 2g(x), \\ \text{iii)}\quad \mu \text{ independent of } x, \end{cases}$$

we have the following

Answers 1) Yes.

2) The asymptotic time dependence is described completely by a computable system of autonomous o.d.e.'s.

First we comment on the assumptions. In Diekmann et al. (preprint 1983) it is shown how (i) arises in a variant of the previous linear model, where one postulates a stochastic division threshold (the chance to undergo fission is determined by the size gained, independent of the time needed to realize this size increase). When energy (from food) is involved in c (ii) is certainly unrealistic, since it ignores the basic metabolism. However, it might apply to phosphate or nitrate limitation since these chemicals are used for building material. Assumptions (i) and (ii) imply that fission stops completely immediately after exhaustion of the substrate and, in principle, this consequence can be tested experimentally. However, a practical complication is formed by the fact that the fission process of each cell takes time (and that it will complete once started) and that, consequently, the instant at which fission stops is difficult to define or measure exactly. (Anyhow, we admit that (ii) is suggested by the fact that it makes mathematical life easy). Finally, (iii) is appropriate in a chemostat. That explains why we took the same μ in (5).

Next, we sketch the analysis of (1) & (5) under assumption (6). Abstractly, we can write the equation for n as

$$\frac{dn}{dt} = -\mu n + \beta(c)An,$$

where A is a linear operator. Let λ_0 be the dominant eigenvalue of A and n_0 the corresponding eigenfunction. Substitute

$$n(t,x) = \rho(t)\,\{n_0(x) + n_1(t,x)\}, \tag{7}$$

where n_1 is in the appropriate complementary subspace. By a trick (based on time scaling; note that under our assumptions growth and division scale in the same way) one can prove that $n_1(t,x) \to 0$ as $t \to +\infty$. Hence we can take limits in the equations for ρ and c to obtain:

$$\begin{cases} \rho' = \rho(\lambda_0\beta(c)-\mu) \\ c' = \gamma - H(c)\rho - \mu c \end{cases} \tag{8}$$

where by definition

$$H(c) = \int_{\frac{1}{2}a}^{1} h(x,c)n_0(x)dx.$$

Note that both λ_0 and H are amenable to numerical calculation. We refer to Diekmann et al. (preprint 1983) for the details and for other feedback mechanisms which can be modelled and analysed in a similar manner.

So, under some rather special assumptions, these complicated models yield o.d.e. systems which can be analysed in all detail. This certainly is encouraging. Theoretically at least, one can relate in this way parameters in an o.d.e. total population model like (8) to (observable?) properties of individuals like growth and fission rates. Whether or not this has any practical significance remains to be seen.

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