SMALL PARAMETERS IN STRUCTURED POPULATION MODELS AND THE TROTTER-KATO THEOREM*

H. J. A. M. HEIJMANS† AND J. A. J. METZ‡

Abstract. The justification of some (often implicit) limit arguments used in the development of structured population models is discussed via two examples. The first example shows how a pair of sink-source terms may transform into a side condition relating the appearance of individuals in the interior of the individual state space to the outflow of individuals at its boundary. The second example considers the usual equation for size-dependent population growth in which it is implicitly assumed that discrete finitely-sized young are produced from infinitesimal contributions by all potential parents. The main mathematical tool for dealing with these examples is the Trotter-Kato theorem for one-parameter semigroups of bounded linear operators.

Key words. structured population, limit transition, C_0-semigroup, Trotter-Kato theorem

AMS(MOS) subject classifications. 92A15, 35A35, 47D05

1. Introduction.

1.1. Biological motivation: structured populations, semigroups of operators, and the need for model simplifications.
The tenet of the *physiologically structured* approach to the modeling of the dynamics of populations as set out in Metz and Diekmann (1986) is that, provided all individuals experience the same environmental inputs such as food availability or chance of running into a predator, we may (and should) represent a population as a frequency distribution over a space Ω of potential states of the individuals comprising the population. (As we frequently need corresponding concepts on the individual and population levels we will, where necessary, use the prefixes *i*- and *p*- to distinguish the corresponding terms, for example *i*-state versus *p*-state, where the latter refers to the frequency distribution.) The main effort in model construction is the determination of an appropriate state representation of *i*-behavior, where the *i*-behavior consists of (i) any contributions to population change such as giving birth or dying, and (ii) any quantities relevant to the calculation of the output from the population model, such as the rate at which the individual consumes food. If we make the assumption that the number of individuals is sufficiently large, then for any given course of the environment the present *p*-state should determine the future *p*-states in a deterministic and linear fashion. For a constant environment the maps relating subsequent *p*-states should form a linear semigroup.

The transition from *i*-model to *p*-model is made through their differential generators. It is here that we leave biology and start doing mathematics: did we really write down a genuine differential generator, and what can be said about the properties of the semigroup so generated?

Until now the attention has been mostly restricted to models where the *i*-state space Ω is a subset of $\mathbb{R}^k$, and where the individuals move through Ω according to the solution of an ordinary differential equation (ODE), possibly alternating with (usually randomly occurring) state jumps, for example, due to an individual losing weight when it splits off a daughter. The reasons for this restriction are twofold. First, models allowing continuous random *i*-state movements contain many more coefficient functions, which are difficult to specify on a mechanistic basis starting from known

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underlying biology. Second, it is generally easier to obtain biological information from less complex models. After all, the goal of the whole exercise is gaining, preferably quantitative, insight into the relation between concrete, though possibly idealized, mechanisms operating in the individuals and consequent population dynamical phenomena. In fact random state jumps are already a bit of a nuisance in that they preclude the sort of simple calculations that a practicing biologist can perform all by himself.

In the present paper we will consider the systematic simplification of two models that both contain random i-state jumps. In the first model, which derives from cell kinetics, we will remove the random character of the jumps by concentrating the takeoffs at one place in Ω only. In the second model, which derives from the population dynamics of ectothermic animals (compare Sinko and Streifer (1967); Streifer (1974); Murphy (1983); Metz, de Roos, and van den Bosch (1988); and in particular Metz and Diekmann (1986)) and also from the dynamics of fungal pellet cultures (compare Edelstein and Hadar (1983); and Chipot and Edelstein (1983)), we will let the size of the jumps become infinitesimally small, while at the same time increasing their occurrence rate. The mathematical tools we use to justify the limit transitions are derived from the theory of one-parameter semigroups of operators (see Pazy (1983)). Particularly important is the Trotter-Kato theorem, which relates the convergence of a sequence of infinitesimal generators (respectively, their resolvents) to the convergence of the associated semigroups. The resulting limit models both allow simple alternative representations in the form of renewal equations for the rates at which newborns appear into the population with kernels, which can easily be calculated in terms of the model ingredients, making possible the routine calculation of biologically relevant quantities such as the asymptotic rate of population increase. Moreover, the limit models contain a smaller number of coefficient functions, making it easier to calibrate them against experimental data.

1.2. Simplification procedures in two special models. In both models considered in this paper the i-state variable of interest will be size; the growth rate of an individual of size x will be denoted as $g(x)$, and Ω will be an interval of $\mathbb{R}_+$. The rate at which individuals of size x die will be denoted as $\mu(x)$.

In the first family of models we consider cells that divide into two at a rate $b_\varepsilon(x)$, where $\varepsilon > 0$ is a small parameter. It is assumed that cells that have passed size one are no longer capable of dividing, but either differentiate or die, i.e., $b_\varepsilon(x) = 0$ for $x > 1$. We will moreover assume that $b_\varepsilon(x) = 0$ for $x < 1 - \varepsilon$. The two daughter cells may differ in size, but the distribution of their relative sizes is constant. This distribution is represented by the probability density $d(p)$, $d : (0, 1) \to \mathbb{R}_+$, where p is the fractional size of the daughter relative to that of its mother. As the sizes of the two daughters add up to the size of the mother, d is symmetric around $\frac{1}{2}$. We will moreover assume that $d(p) = 0$ outside $(\frac{1}{2} - \Delta, \frac{1}{2} + \Delta)$. Finally we assume that ε is so small that the size of the largest newborn daughter is less than the size of the smallest mother, i.e., $\frac{1}{2} + \Delta < 1 - \varepsilon$. Then the size of the smallest daughter, x_{min}, satisfies

$$x_{min} = (1 - \varepsilon)(\tfrac{1}{2} - \Delta) > (\tfrac{1}{2} + \Delta)(\tfrac{1}{2} - \Delta) =: \alpha.$$

This allows us to choose Ω to be $[\alpha, 1]$ independent of ε. The growth rate g is assumed to be positive and continuous on Ω. Let $n(t, \cdot)$ denote the density function of the cell sizes present at time t; then

(1.1a) $\quad \dfrac{\partial}{\partial t} n(t, x) = -\dfrac{\partial}{\partial x}(g(x)n(t, x)) - b_\varepsilon(x)n(t, x) + 2 \displaystyle\int_0^1 \dfrac{d(p)}{p} b_\varepsilon\left(\dfrac{x}{p}\right) n\left(t, \dfrac{x}{p}\right) dp,$

(1.1b) $\quad n(t, \alpha) = 0.$

Now assume that when we let $\varepsilon \downarrow 0$, the quantity

$$\int_{1-\varepsilon}^{1} \frac{b_\varepsilon(y)}{g(y)} \, dy$$

converges to a number larger than zero. This means that the probability that a newborn cell is eventually going to divide

$$(1.2) \qquad \pi_\varepsilon = 1 - \exp\left(-\int_{1-\varepsilon}^{1} \frac{b_\varepsilon(y)}{g(y)} \, dy\right)$$

converges to a value $\pi_0 > 0$. In the limit cells will only divide on reaching $x = 1$, and they do so with probability π_0. The corresponding population equation is

$$(1.3a) \qquad \frac{\partial}{\partial t} n(t, x) = -\frac{\partial}{\partial x}(g(x)n(t, x)) + 2d(x)\pi_0 g(1)n(t, 1),$$

$$(1.3b) \qquad n(t, \alpha) = 0.$$

This limit model may be used as a convenient approximation when cell division occurs only in a narrow size window.

In §2 we show that under suitable assumptions on the functions g, d, and b_ε, the solutions of (1.1) on the space $L^1[\alpha, 1]$ indeed converge to the solutions of (1.3).

In the second family of models we consider individuals that reproduce at a rate $\beta_\varepsilon(x)$ by splitting off young with size ε, ε small, while concurrently their size is decreased by the same amount. We assume that newborns have viability ρ_ε due to the necessity to survive an infinitesimally short larval stage. The corresponding population equation reads as follows:

$$(1.4a) \qquad \frac{\partial n}{\partial t}(t, x) + \frac{\partial}{\partial x}(g(x)n(t, x)) = -\beta_\varepsilon(x)n(t, x) + \beta_\varepsilon(x + \varepsilon)n(t, x + \varepsilon) - \mu(x)n(t, x),$$

$$(1.4b) \qquad g(\varepsilon +)n(t, \varepsilon +) - g(\varepsilon -)n(t, \varepsilon -) = \rho_\varepsilon \int_0^1 \beta_\varepsilon(x)n(t, x) \, dx,$$

$$(1.4c) \qquad g(0)n(t, 0) = 0,$$

$$(1.4d) \qquad n(0, x) = \psi(x).$$

In (1.4b),

$$g(\varepsilon +)n(t, \varepsilon +) - g(\varepsilon -)n(t, \varepsilon -) = \lim_{h \downarrow 0}[g(\varepsilon + h)n(t, \varepsilon + h) - g(\varepsilon - h)n(t, \varepsilon - h)].$$

It is assumed that growth stops at $x = 1$, i.e., $g(1) = 0$, and that g is positive for all smaller sizes including zero. Although the model structure is still compatible with representing the population state as a density function $n(t, \cdot)$, the *jump condition* (1.4b) makes the problem technically troublesome. A natural way out of this dilemma is provided by the observation that the only interesting quantities to be derived from a structured population model are population averages such as total population size, total biomass, or population feeding rate, i.e., linear functionals of $n(t, \cdot)$. This brings us to consider the so-called backward equation

$$(1.5a) \qquad \begin{aligned} &\frac{\partial m}{\partial t}(t, x) - g(x)\frac{\partial m}{\partial x}(t, x) \\ &= -\beta_\varepsilon(x)m(t, x) + \beta_\varepsilon(x)m(t, x - \varepsilon) + \rho_\varepsilon\beta_\varepsilon(x)m(t, \varepsilon) - \mu(x)m(t, x), \end{aligned}$$

$$(1.5b) \qquad m(0, x) = \phi(x),$$

satisfied by the clan averages

$$(1.6) \qquad m(t, x) = \int_0^1 \phi(\xi) N_x(t, d\xi),$$

where the Borel measure $N_x(t, \cdot)$ represents the expected state at time t of a clan descending from an ancestral individual sized x at time zero. If $m_\varepsilon(t, x; \phi)$ is the solution of (1.5), then every p-output is of the form $\int_0^1 m_\varepsilon(t, x; \phi)\psi(dx)$, where ψ is the initial condition in (1.4d). In § 3.3 we give a precise description of the duality relation between solutions of the forward and backward equations in terms of semigroups and generators (also see Heijmans (1984) and Clement et al. (1987)).

In nature usually roughly the same amount of energy is available for reproduction, which, depending on the species, may be spent on producing a few large or many small young. Therefore we set

$$(1.7) \qquad \beta_\varepsilon(x) = \varepsilon^{-1} b(x).$$

Moreover, in species with many small young, infant mortality is generally much higher than when the young are large. If recruitment is to stay bounded when we let ε go to zero we have to put

$$(1.8) \qquad \rho_\varepsilon = \varepsilon r.$$

Inserting (1.7) and (1.8) into (1.5a) and letting $\varepsilon \downarrow 0$, we obtain

$$(1.9) \qquad \frac{\partial m}{\partial t}(t, x) - (g(x) - b(x))\frac{\partial m}{\partial x}(t, x) = rb(x)m(t, 0) - \mu(x)m(t, x),$$

which corresponds to the forward equation

$$(1.10) \qquad \begin{aligned} \frac{\partial}{\partial t} n(t, x) &= -\frac{\partial}{\partial x}(\gamma(x)n(t, x)) - \mu(x)n(t, x), \\ \gamma(x_0)n(t, x_0) &= \int rb(y)n(t, y) \, dy, \end{aligned}$$

with

$$(1.11) \qquad \gamma(x) = g(x) - b(x)$$

and $x_0 = 0$. Instead of being set back in size at each discrete reproductive event the individual's growth rate is reduced by an amount related to the energy spent in reproduction. Note that in contrast to g the reduced growth rate γ is no longer positive on $[0, 1)$, in particular $\gamma(1) = -b(1) < 0$.

In § 3.2 we show that under suitable assumptions on the functions g, b, and μ, the semigroup generated by (1.5) indeed converges to the semigroup generated by (1.9). In that section we will also discuss in somewhat more detail the relation between the forward and backward equations.

Equation (1.10) is the equation usually encountered in the population dynamical literature; only x_0 is generally assumed to be positive. Biologically this amounts to the assumption that either parents can time and again produce instantaneously additional masses x_0, notwithstanding the fact that they can add to their own body mass only in a continuous fashion, or else that live newborns are created by magic out of the added infinitesimal contributions by all parents together. Both assumptions go against the grain. Our limiting procedure provides a possible justification, provided x_0 is vanishingly small.

Note for the biological reader. There remains the seemingly awkward assumption that $g(0) > 0$. However, the most often encountered biological growth law, the Von Bertalanffy equation, has precisely this property. Note that the Von Bertalanffy Ansatz does not allow individuals to spontaneously spring into being by growing away from size zero. What matters is that $\lim_{x \downarrow 0} g(x) > 0$. Individuals of size zero never exist, only individuals that are very small.

Remark. Another way to guarantee that recruitment stays bounded for $\varepsilon \downarrow 0$ is to keep ρ_ε constant and to replace the usual integrability assumption on μ by the assumption that

$$\frac{\mu(x)}{g(x)} = \frac{1}{x} + f(x)$$

with f an L^1 function. To see that this has indeed the intended effect, observe that the probability that a recruited individual survives until it reaches size $x > \varepsilon$ equals

$$\exp\left(-\int_\varepsilon^x \frac{\mu(y)}{g(y)} \, dy\right).$$

(Note that any other choice for the behavior of $\mu(x)$ near $x = 0$ does not for $\varepsilon \downarrow 0$ yield the needed survival proportional to ε during the first moments after recruitment!)

2. From distributed to concentrated division.

2.1. The equation and the associated semigroup. In this section we make a thorough mathematical study of (1.1) describing a size-structured cell population reproducing by division. For the sake of convenience we recall the following equation:

$$(2.1a) \quad \frac{\partial n}{\partial t}(t, x) + \frac{\partial}{\partial x}(g(x)n(t, x)) = -b_\varepsilon(x)n(t, x) + 2\int_0^1 \frac{d(p)}{p} b_\varepsilon\left(\frac{x}{p}\right)n\left(t, \frac{x}{p}\right) dp,$$

$$(2.1b) \quad n(t, \alpha) = 0,$$

$$(2.1c) \quad n(0, x) = \phi(x).$$

We will prove that under the right set of assumptions solutions of this problem converge for $\varepsilon \downarrow 0$ to solutions of the limit equation (1.3), i.e.,

$$(2.2a) \qquad \frac{\partial n}{\partial t}(t, x) + \frac{\partial}{\partial x}(g(x)n(t, x)) = 2\pi_0 d(x)g(1)n(t, 1),$$

$$(2.2b) \qquad n(t, a) = 0,$$

$$(2.2c) \qquad n(0, x) = \phi(x).$$

We refer to § 1.2 for the interpretation of ε, g, b_ε, d, α, and π_0. As the underlying population state space we choose $X = L^1[\alpha, 1]$. We make the following assumptions.

Assumption 2.1. (a) $g \in C[\alpha, 1]$; $g(x) > 0, x \in [\alpha, 1]$.

(b) $d \in C[0, 1]$; $d(p) > 0$ if and only if $|p - \frac{1}{2}| < \Delta$; d is symmetric around $p = \frac{1}{2}$, and $\int_{1/2-\Delta}^{1/2+\Delta} d(p) \, dp = 1$.

(c) $b_\varepsilon \in C[\alpha, 1]$; $b_\varepsilon(x) = 0, x \in [\alpha, 1 - \varepsilon]$; $b_\varepsilon(x) > 0, x \in (1 - \varepsilon, 1]$.

We can write (2.1) with initial condition $\phi \in X$ as the abstract Cauchy problem

$$(2.3) \qquad \frac{dn}{dt}(t) = A_\varepsilon n(t), \qquad n(0) = \phi,$$

where the closed operator A_ε on X is given by

$$(2.4) \quad (A_\varepsilon \phi)(x) = -\frac{d}{dx}(g(x)\phi(x)) - b_\varepsilon(x)\phi(x) + 2\int_{1/2-\Delta}^{1/2+\Delta} \frac{d(p)}{p} b_\varepsilon\left(\frac{x}{p}\right)\phi\left(\frac{x}{p}\right) dp,$$

for any ϕ in its domain

(2.5) $\qquad D(A_\varepsilon) = \{\phi \in X : g\phi \in W^{1,1}[\alpha, 1]$ and $\phi(\alpha) = 0\}$.

Using a standard perturbation result for C_0-semigroups (Pazy (1983, § 3.1)) we easily show that A_ε is the infinitesimal generator of a strongly continuous semigroup $\{T_\varepsilon(t)\}_{t \geq 0}$.

Let A be a closed linear operator on the Banach space X and let $M \geq 0$, $\omega \in \mathbb{R}$. We say that $A \in G(M, \omega)$ if A is the infinitesimal generator of a C_0-semigroup $\{T(t)\}_{t \geq 0}$ of bounded linear operators satisfying

$$\|T(t)\| \leq M e^{\omega t}, \qquad t \geq 0$$

(e.g., Pazy (1983, § 3.4)). The next proposition states, among other things, that there exists a semigroup solution to (2.1).

THEOREM 2.2. *There exist constants* $\omega \in \mathbb{R}$ *and* $M \geq 1$ (*which do not depend on* ε), *such that* $A_\varepsilon \in G(M, \omega)$.

Proof. Let $\| \cdot \|$ be the L^1-norm. Then the norm $\| \cdot \|$ is equivalent to the norm $\| \cdot \|'$ given by

$$\|\phi\|' = \int_\alpha^1 x|\phi(x)| \, dx, \qquad \phi \in X.$$

Let, for $t \geq 0$,

$$\|T_\varepsilon(t)\|' = \sup\{\|T_\varepsilon(t)\phi\|'/\|\phi\|' : \phi \in X, \phi \neq 0\}.$$

Since $T_\varepsilon(t)$ is a positive operator, we have

$$\|T_\varepsilon(t)\|' = \{\|T_\varepsilon(t)\phi\|'/\|\phi\|' : \phi \in X_+, \phi \neq 0\},$$

where X_+ is the cone of positive elements. If $\phi \in X_+$, then $\|T_\varepsilon(t)\phi\|' = \int_\alpha^1 xn(t, x) \, dx$, where $n(t, x)$ is the solution of (2.1). If, in addition, $\phi \in D(A_\varepsilon)$, then

$$\frac{d}{dt} \int_\alpha^1 xn(t, x) \, dx \leq \int_\alpha^1 g(x)n(t, x) \, dx \leq \omega \int_\alpha^1 xn(t, x) \, dx,$$

where $\omega > 0$ is taken so large that $g(x) \leq \omega x$, $x \in [\alpha, 1]$. So for $\phi \in D(A_\varepsilon) \cap X_+$ we find that

$$\|T_\varepsilon(t)\phi\|' = \int_\alpha^1 xn(t, x) \, dx \leq e^{\omega t} \int_\alpha^1 x\phi(x) \, dx = e^{\omega t}\|\phi\|'.$$

Since $D(A_\varepsilon) \cap X_+$ is norm-dense in X_+, this holds for any $\phi \in X_+$, and we find that

$$\|T_\varepsilon(t)\|' \leq e^{\omega t}, \qquad t \geq 0.$$

Since $\| \cdot \|'$ and $\| \cdot \|$ are equivalent norms, there exists a constant $M > 0$ such that

$$\|T_\varepsilon(t)\| \leq M e^{\omega t}, \qquad t \geq 0,$$

and the result is proved. □

2.2. Justification of the limit transition. In this section we give a formal mathematical justification of the limit transition $\varepsilon \downarrow 0$ which amounts to (2.2). That is to say, we prove that the solution of (2.1) given by $n(t, \cdot) = T_\varepsilon(t)\phi$ converges to the solution of (2.2) as $\varepsilon \downarrow 0$. For this purpose, we use the Trotter-Kato theorem. Besides Assumptions 2.1(a)–(c) we only assume there exists a $\pi_0 \in [0, 1)$ such that $\lim_{\varepsilon \downarrow 0} \pi_\varepsilon = \pi_0$.

We rewrite (2.2) as the abstract Cauchy problem

$$(2.6) \qquad \frac{dn}{dt}(t) = An(t), \qquad n(0) = \phi,$$

where A is the closed operator

$$(2.7) \qquad (A\phi)(x) = -\frac{d}{dx}(g(x)\phi(x)) + 2\pi_0 d(x)g(1)\phi(1)$$

with dense domain

$$(2.8) \qquad D(A) = \{\phi \in X: g\phi \in W^{1,1}[\alpha, 1] \text{ and } \phi(\alpha) = 0\}.$$

THEOREM 2.3. *For* $\lambda \in \mathbb{R}$ *large enough we have*

$$R(\lambda, A_\varepsilon)\phi \to R(\lambda, A)\phi, \qquad \varepsilon \downarrow 0,$$

for every $\phi \in X$.

Proof. The proof consists of four steps.

(1) Let the isomorphism $U_\varepsilon: X \to X$ be given by

$$(U_\varepsilon\phi)(x) = \frac{E_\varepsilon(x)}{g(x)}\phi(x),$$

where $E_\varepsilon(x) = \exp\left(-\int_\alpha^x (b_\varepsilon(y)/g(y))\, dy\right)$. Let

$$D = D(A) = D(A_\varepsilon) = \{\phi \in X: g\phi \in W^{1,1}[\alpha, 1] \text{ and } \phi(\alpha) = 0\},$$

and

$$\tilde{D} = U_\varepsilon^{-1}D = \{\phi \in X: \phi \in W^{1,1}[\alpha, 1] \text{ and } \phi(\alpha) = 0\}.$$

Let $\tilde{A}_\varepsilon$ be the closed operator $U_\varepsilon^{-1}A_\varepsilon U_\varepsilon$ with domain $D(\tilde{A}_\varepsilon) = \tilde{D}$. Then $\tilde{A}_\varepsilon$ is given by

$$(\tilde{A}_\varepsilon\phi)(x) = -g(x)\frac{d\phi}{dx}(x) + 2\frac{g(x)}{E_\varepsilon(x)}\int_{1/2-\Delta}^{1/2+\Delta}\frac{d(p)}{p}r_\varepsilon\left(\frac{x}{p}\right)\phi\left(\frac{x}{p}\right)\, dp,$$

where $r_\varepsilon(x) = (b_\varepsilon(x)/g(x))E_\varepsilon(x)$ for $x \in [\alpha, 1]$. We define the isomorphism $U: X \to X$ by

$$(U\phi)(x) = \frac{\phi(x)}{g(x)}.$$

Let $\tilde{A}$ be the closed operator $U^{-1}AU$ with domain $D(\tilde{A}) = U^{-1}D = \tilde{D}$. For $\phi \in D(\tilde{A})$ we have

$$(\tilde{A}\phi)(x) = -g(x)\frac{d\phi}{dx}(x) + 2\pi_0 d(x)g(x)\phi(1).$$

(2) We show that for every $\phi \in \tilde{D}$,

$$\tilde{A}_\varepsilon\phi \to \tilde{A}\phi \quad \text{as } \varepsilon \downarrow 0.$$

Let $\phi \in \tilde{D}$, then

$$(\tilde{A}_\varepsilon\phi)(x) - (\tilde{A}\phi)(x) = 2\frac{g(x)}{E_\varepsilon(x)}\int_{1/2-\Delta}^{1/2+\Delta}\frac{d(p)}{p}r_\varepsilon\left(\frac{x}{p}\right)\phi\left(\frac{x}{r}\right)\, dp - 2\pi_0 d(x)g(x)\phi(1).$$

We define $\bar{g} = \max_{x \in [\alpha, 1]} g(x)$, $\bar{d} = \max_{p \in [1/2 - \Delta, 1/2 + \Delta]} d(p)$. Now

$$\|\tilde{A}_\varepsilon \phi - \tilde{A} \phi\| = \int_\alpha^1 \left| \frac{2g(x)}{E_\varepsilon(x)} \int_{1/2 - \Delta}^{1/2 + \Delta} \frac{d(p)}{p} r_\varepsilon \left(\frac{x}{p}\right) \phi \left(\frac{x}{p}\right) dp - 2\pi_0 \, d(x) g(x) \phi(1) \right| dx$$

$$= \int_{(1/2 - \Delta)(1 - \varepsilon)}^{1/2 + \Delta} \left| 2g(x) \int_{1/2 - \Delta}^{1/2 + \Delta} \frac{d(p)}{p} r_\varepsilon \left(\frac{x}{p} \phi \left(\frac{x}{p}\right)\right) dp - 2\pi_0 \, d(x) g(x) \phi(1) \right| dx$$

$$\leqq 2\bar{g} \int_{(1/2 - \Delta)(1 - \varepsilon)}^{1/2 + \Delta} \left| \int_{1/2 - \Delta}^{1/2 + \Delta} \frac{d(p)}{p} r_\varepsilon \left(\frac{x}{p}\right) \phi \left(\frac{x}{p}\right) dp - \pi_\varepsilon \, d(x) \phi(1) \right| dx$$

$$+ 2\bar{g} \left| \pi_\varepsilon - \pi_0 \right| \cdot \left| \phi(1) \right|.$$

This second expression at the right-hand side can easily be estimated. We write the first expression as the sum of three integrals:

$$\int_{(1/2 - \Delta)(1 - \varepsilon)}^{1/2 + \Delta} = \int_{(1/2 - \Delta)(1 - \varepsilon)}^{1/2 - \Delta} + \int_{1/2 - \Delta}^{(1/2 + \Delta)(1 - \varepsilon)} + \int_{(1/2 + \Delta)(1 - \varepsilon)}^{1/2 + \Delta}.$$

It is the middle integral that causes the most trouble, and we restrict our attention to this term. Let $\delta > 0$:

$$2\bar{g} \int_{1/2 - \Delta}^{(1/2 + \Delta)(1 - \varepsilon)} \left| \int_{1/2 - \Delta}^{1/2 + \Delta} \frac{d(p)}{p} r_\varepsilon \left(\frac{x}{p}\right) \phi \left(\frac{x}{p}\right) dp - \pi_\varepsilon \, d(x) \phi(1) \right| dx$$

$$= 2\bar{g} \int_{1/2 - \Delta}^{(1/2 + \Delta)(1 - \varepsilon)} \left| \int_{x/(1/2 + \Delta)}^{x/(1/2 - \Delta)} \frac{1}{y} d \left(\frac{x}{y}\right) r_\varepsilon(y) \phi(y) \, dy - \pi_\varepsilon \, d(x) \phi(1) \right| dx$$

$$= 2\bar{g} \int_{1/2 - \Delta}^{(1/2 + \Delta)(1 - \varepsilon)} \left| \int_{1 - \varepsilon}^1 \frac{1}{y} d \left(\frac{x}{y}\right) r_\varepsilon(y) \phi(y) \, dy - \int_{1 - \varepsilon}^1 d(x) r_\varepsilon(y) \phi(1) \, dy \right| dx$$

$$= 2\bar{g} \int_{1/2 - \Delta}^{(1/2 + \Delta)(1 - \varepsilon)} \left| \int_{1 - \varepsilon}^1 \left\{ \frac{1}{y} d \left(\frac{x}{y}\right) \phi(y) - \frac{1}{1} d \left(\frac{x}{1}\right) \phi(1) \right\} r_\varepsilon(y) \, dy \right| dx$$

$$\leqq 2\bar{g} \int_{1/2 - \Delta}^{(1/2 + \Delta)(1 - \varepsilon)} \left\{ \int_{1 - \varepsilon}^1 \delta r_\varepsilon(y) \, dy \right\} dx \leqq 2\bar{g} \cdot 2\Delta \cdot \delta.$$

Here we have chosen $\varepsilon > 0$ so small that

$$\left| \frac{1}{y} d \left(\frac{x}{y}\right) \phi(y) - \frac{1}{1} d \left(\frac{x}{1}\right) \phi(1) \right| < \delta,$$

for every $x \in [\frac{1}{2} - \Delta, (\frac{1}{2} + \Delta)(1 - \varepsilon)]$ and $y \in [1 - \varepsilon, 1]$, and we used that $\int_{1 - \varepsilon}^1 r_\varepsilon(y) \, dy = \pi_\varepsilon \leqq 1$. This shows that $\tilde{A}_\varepsilon \phi \to \tilde{A} \phi$ as $\varepsilon \downarrow 0$, for $\phi \in \tilde{D}$.

(3) We show that for $\lambda \in \mathbb{R}$ large enough (in particular $\lambda > \omega$; see Theorem 2.2)

$$R(\lambda, \tilde{A}_\varepsilon) \phi \to R(\lambda, \tilde{A}) \phi \quad \text{as } \varepsilon \downarrow 0,$$

for every $\phi \in X$. Choose $\lambda > \omega$ so large that $\lambda \in \rho(A) = \rho(\tilde{A})$. Let $\phi \in X$, and define $\psi \in \tilde{D}$ as $\psi = R(\lambda, \tilde{A})\phi$. For $\varepsilon > 0$, let $\phi_\varepsilon = (\lambda - \tilde{A}_\varepsilon)\psi$. From

$$\tilde{A}_\varepsilon \psi \to \tilde{A} \psi \quad \text{as } \varepsilon \downarrow 0$$

we get $\phi_\varepsilon \to \phi$ as $\varepsilon \downarrow 0$. Since $R(\lambda, \tilde{A}_\varepsilon) = U_\varepsilon^{-1} R(\lambda, A_\varepsilon) U_\varepsilon$, we deduce from Theorem 2.2 that

$$\|R(\lambda, \tilde{A}_\varepsilon)\| \le \frac{\tilde{M}}{\lambda - \omega}, \quad \varepsilon > 0.$$

Here we have used explicitly that $\pi_0 < 1$. Now

$$\lim_{\varepsilon \downarrow 0} R(\lambda, \tilde{A}_\varepsilon)\phi = \lim_{\varepsilon \downarrow 0} [R(\lambda, \tilde{A}_\varepsilon)(\phi - \phi_\varepsilon) + \psi] = \psi = R(\lambda, \tilde{A})\phi.$$

(4) We finally show that for $\lambda \in \mathbb{R}$ large enough,

$$R(\lambda, A_\varepsilon)\phi \to R(\lambda, A)\phi \quad \text{as } \varepsilon \downarrow 0,$$

for every $\phi \in X$. It is easily checked that

$$U_\varepsilon \phi \to U\phi, \quad \varepsilon \downarrow 0 \quad \text{and} \quad U_\varepsilon^{-1}\phi \to U^{-1}\phi, \quad \varepsilon \downarrow 0,$$

for every $\phi \in X$, and that there exists a constant $L > 0$ such that $\|U_\varepsilon\|$, $\|U\|$, $\|U_\varepsilon^{-1}\|$, $\|U^{-1}\| \le L$, $\varepsilon > 0$. For every $\phi \in X$ we have

$$\|R(\lambda, A_\varepsilon)\phi - R(\lambda, A)\phi\| = \|U_\varepsilon R(\lambda, \tilde{A}_\varepsilon) U_\varepsilon^{-1}\phi - UR(\lambda, A)U^{-1}\phi\|$$

$$= \|(U_\varepsilon - U)(R(\lambda, \tilde{A}_\varepsilon) U_\varepsilon^{-1} - R(\lambda, \tilde{A}_\varepsilon)U^{-1} + R(\lambda, \tilde{A}_\varepsilon)U^{-1}$$

$$- R(\lambda, \tilde{A})U^{-1} + R(\lambda, \tilde{A})U^{-1})\phi$$

$$+ U(R(\lambda, \tilde{A}_\varepsilon) - R(\lambda, \tilde{A}))(U_\varepsilon^{-1} - U^{-1} + U^{-1})\phi$$

$$+ UR(\lambda, \tilde{A})(U_\varepsilon^{-1} - U^{-1})\phi\|$$

$$\le \|U_\varepsilon - U\| \|R(\lambda, \tilde{A}_\varepsilon)\| \|U_\varepsilon^{-1}\phi - U^{-1}\phi\|$$

$$+ \|U_\varepsilon - U\| \|R(\lambda, \tilde{A}_\varepsilon)U^{-1}\phi - R(\lambda, \tilde{A})U^{-1}\phi\|$$

$$+ \|(U_\varepsilon - U)R(\lambda, \tilde{A})U^{-1}\phi\|$$

$$+ \|U\| \|R(\lambda, \tilde{A}_\varepsilon) - R(\lambda, \tilde{A})\| \|U_\varepsilon^{-1}\phi - U^{-1}\phi\|$$

$$+ \|U\| \|(R(\lambda, \tilde{A}_\varepsilon) - R(\lambda, \tilde{A}))U^{-1}\phi\|$$

$$+ \|U\| \|R(\lambda, \tilde{A})\| \|U_\varepsilon^{-1}\phi - U^{-1}\phi\|,$$

and all these terms go to zero as $\varepsilon \downarrow 0$. $\square$

We can now apply the Trotter-Kato theorem (Pazy (1983, § 3.4)), which yields that (i) A is the infinitesimal generator of a C_0-semigroup (in particular this means that (2.2) is well posed) and that (ii) the solution of (2.1) converges to the solution of (2.2) as $\varepsilon \downarrow 0$.

THEOREM 2.4. $A \in G(M, \omega)$, and if $\{T(t)\}_{t \ge 0}$ is the semigroup generated by A, then for every $\phi \in X$, $t \ge 0$,

$$T_\varepsilon(t)\phi \to T(t)\phi \quad \text{as } \varepsilon \downarrow 0.$$

Moreover, the convergence is uniform with respect to t in bounded subsets of $(0, \infty)$.

3. From size jumps to reduced growth.

3.1. The semigroup solution to the backward equation.
In this section we show that under some reasonable assumptions we can associate a C_0-semigroup of bounded linear operators on $X = C[0, 1]$ with the backward equation (1.5), which we recall below for convenience. Throughout this section we will assume that the death rate μ

is identically zero. However, all the results obtained here remain valid for nonzero death rates. The backward equation reads as follows:

$$(3.1a) \quad \frac{\partial m}{\partial t}(t, x) - g(x)\frac{\partial m}{\partial x}(t, x) = -\beta_\varepsilon(x)n(t, x) + \beta_\varepsilon(x)m(t, x - \varepsilon) + \rho_\varepsilon\beta_\varepsilon(x)m(t, \varepsilon),$$

$$(3.1b) \quad m(0, x) = \phi(x).$$

Assumption 3.1. (a) g is Lipschitz continuous on $[0, 1]$; $g(x) > 0$, $x \in [0, 1)$; $g(1) = 0$.

(b) β_ε is Lipschitz continuous on $[0, 1]$; there is an $a > \varepsilon$ such that $\beta_\varepsilon(x) = 0$, $x \in [0, a]$ and $\beta_\varepsilon(x) > 0$, $x \in (a, 1]$.

Here a denotes the minimum size at which an individual can reproduce. We can write (3.1) as the abstract Cauchy problem:

$$(3.2a) \qquad\qquad \frac{dm}{dt}(t) = A_\varepsilon m(t),$$

$$(3.2b) \qquad\qquad m(0) = \phi \in X,$$

where the closed unbounded operator A_ε with domain

$$D(A_\varepsilon) = \{\phi \in X \cap W^{1,1}_{loc}[0, 1] : g\phi' \in X\},$$

is given by

$$(A_\varepsilon\phi)(x) = g(x)\frac{d\phi}{dx}(x) - \beta_\varepsilon(x)\phi(x) + \beta_\varepsilon(x)\phi(x - \varepsilon) + \rho_\varepsilon\beta_\varepsilon(x)\phi(\varepsilon).$$

We write A_ε as the sum of two operators:

$$(3.3) \qquad\qquad A_\varepsilon = A_0 + B_\varepsilon,$$

where the closed unbounded operator A_0 has the same domain as A_ε and is given by

$$(A_0\phi)(x) = g(x)\frac{d\phi}{dx}(x),$$

and where B_ε is a bounded operator given by

$$(B_\varepsilon\phi)(x) = -\beta_\varepsilon(x)\phi(x) + \beta_\varepsilon(x)\phi(x - \varepsilon) + \rho_\varepsilon\beta_\varepsilon(x)\phi(\varepsilon).$$

It is quite easy to show that A_0 generates a strongly continuous semigroup $\{T_0(t)\}_{t \geq 0}$, and therefore A_ε, being a bounded perturbation of A_0, also generates a strongly continuous semigroup $\{T_\varepsilon(t)\}_{t \geq 0}$ (see Pazy (1983, § 3.1)).

Both $\{T_0(t)\}_{t \geq 0}$ and $\{T_\varepsilon(t)\}_{t \geq 0}$ are positive semigroups, which is intuitively clear from the biological interpretation, but can also be shown rigorously (see Heijmans (1986)). Let **1** be the element of X that is identically one on $[0, 1]$. Then

$$A_\varepsilon \mathbf{1} = \rho_\varepsilon\beta_\varepsilon.$$

Define the positive scalar ω_ε by

$$(3.4) \qquad\qquad \omega_\varepsilon = \sup\{\rho_\varepsilon\beta_\varepsilon(x) : x \in [0, 1]\}.$$

We see immediately that

$$0 \leq A_\varepsilon \mathbf{1} \leq \omega_\varepsilon \mathbf{1}.$$

We show that $A_\varepsilon \in G(1, \omega_\varepsilon)$. First suppose that $\omega_\varepsilon < s(A_\varepsilon)$, where $s(A_\varepsilon)$ is the spectral bound of A_ε, i.e., $s(A_\varepsilon) = \sup \{\operatorname{Re} \lambda : \lambda \in \sigma(A_\varepsilon)\}$. Since $\{T_\varepsilon(t)\}_{t \geq 0}$ is a positive semigroup, $s(A_\varepsilon) \in \sigma(A_\varepsilon)$ if $\sigma(A_\varepsilon) \neq \varnothing$, and $R(\lambda, A_\varepsilon)$ is a positive operator if $\lambda > s(A_\varepsilon)$ (see Nagel (1986)). Choose $\lambda > s(A_\varepsilon)$. Since $R(\lambda, A_\varepsilon)$ is a positive operator we get that

$$0 \leq R(\lambda, A_\varepsilon)1 \leq \frac{1}{\lambda - \omega_\varepsilon} 1;$$

hence $\|R(\lambda, A_\varepsilon)\| = \|R(\lambda, A_\varepsilon)1\| \leq 1/(\lambda - \omega_\varepsilon)$, and we find that $\|R(\lambda, A_\varepsilon)\|$ remains bounded if $\lambda \downarrow s(A_\varepsilon)$, which is in contradiction with

$$s(A_\varepsilon) \in \sigma(A_\varepsilon).$$

Therefore $\omega_\varepsilon \geq s(A_\varepsilon)$. Using the same arguments as above, we find that for $\lambda > \omega_\varepsilon$,

$$\|R(\lambda, A_\varepsilon)\| \leq \frac{1}{\lambda - \omega_\varepsilon},$$

which yields that for $n = 1, 2, \cdots$

$$\|R(\lambda, A_\varepsilon)^n\| \leq \frac{1}{(\lambda - \omega_\varepsilon)^n},$$

and it follows from the Hille–Yosida theorem that $A_\varepsilon \in G(1, \omega_\varepsilon)$. In particular this implies that A_ε is the generator of a C_0-semigroup $\{T_\varepsilon(t)\}_{t \geq 0}$ on X.

3.2. The limit transition justified. Assuming (1.7) and (1.8), i.e., $\beta_\varepsilon(x) = \varepsilon^{-1}b(x)$ and $\rho_\varepsilon = \varepsilon r$, we find the limiting equation

$$(3.5\text{a}) \qquad \frac{\partial m}{\partial t}(t, x) - \gamma(x)\frac{\partial m}{\partial x}(t, x) = rb(x)m(t, 0),$$

$$(3.5\text{b}) \qquad m(0, x) = \phi(x),$$

where γ is the *reduced growth rate*

$$(3.6) \qquad\qquad\qquad \gamma(x) = g(x) - b(x).$$

Note that it follows from Assumption 3.1 that (i) b is Lipschitz continuous on $[0, 1]$, $b(x) = 0$ for $x \leq a$ and $b(x) > 0$ for $a < x \leq 1$, and that (ii) γ is *not* positive on the whole interval $[0, 1]$, in particular $\gamma(1) = -b(1) < 0$.

In the rest of this section we will show how the Trotter–Kato theorem can be used to justify the formal transition from (3.1)–(3.5). In the next section we interpret these results in terms of the forward equations (1.4) and (1.10) (with $x_0 = 0$).

First we reformulate (3.5a) supplied with initial condition (3.5b) as an abstract Cauchy problem:

$$(3.7) \qquad\qquad \frac{dm}{dt}(t) = Am(t), \qquad m(0) = \phi \in X,$$

where the closed operator A is given by

$$(A\phi)(x) = \gamma(x)\frac{d\phi}{dx}(x) + rb(x)\phi(0)$$

for every ϕ in its domain

$$D(A) = \{\phi \in X \cap W^{1,1}_{\mathrm{loc}}[0, 1] : \gamma\phi' \in X\}.$$

It is not difficult to show that A generates a strongly continuous positive semigroup: this, however, will also follow from the forthcoming analysis. Let

(3.8) $\omega := \{rb(x): 0 \leqq x \leqq 1\}.$

Obviously, $\omega_\varepsilon = \omega$ and from the results of § 3.1 it follows that

(3.9) $A_\varepsilon \in G(1, \omega).$

Assumption 3.2. There exists a unique $\hat{x} \in (0, 1)$ such that $g(\hat{x}) = b(\hat{x})$.
In combination with the other assumptions of this section this means that

$$\gamma(x) > 0, \qquad 0 \leqq x < \hat{x},$$

$$\gamma(x) < 0, \qquad \hat{x} < x \leqq 1.$$

Now let $D = C^1[0, 1]$, i.e., the subspace of X containing all continuously differentiable functions on $[0, 1]$. Clearly

$$D(A_\varepsilon) \subseteq D, \qquad D(A) \subseteq D.$$

PROPOSITION 3.3. $(\lambda - A)D$ *is dense in X for* $\lambda \in \mathbb{R}$ *sufficiently large.*
Proof. Consider for $F \in X$ the inhomogeneous equation

$$\lambda \phi(x) - \gamma(x) \phi'(x) = F(x),$$

where $\lambda \in \mathbb{R}$ is sufficiently large ($\lambda > \omega$). The solution of this equation for $0 \leqq x < \hat{x}$ is given by

(*) $$\phi(x) = \int_x^{\hat{x}} \frac{F(y)}{\gamma(y)} \exp\left\{ -\lambda \int_x^y \frac{d\xi}{\gamma(\xi)} \right\} dy,$$

and a similar expression can be found for $\phi(x)$, if x is greater than $\hat{x}$. It is easy to check that $\phi \in D$ if $F \in D$. Now, for $f \in X$, the solution of

(**) $\lambda \phi - A\phi = f,$

on $(0, \hat{x})$ is given by (*), with $F(x) = f(x) + r\phi(0)b(x)$ substituted. Hence $\phi \in D$ if $F \in D$. Let $f \in X$ and let ϕ be the solution of (**); then

$$\phi(0) = \int_0^{\hat{x}} \frac{f(y) + r\phi(0)b(y)}{\gamma(y)} \exp\left\{ -\lambda \int_0^y \frac{d\xi}{\gamma(\xi)} \right\} dy.$$

We assume that $\lambda \in \mathbb{R}$ is so large that

$$\alpha_\lambda := \int_0^{\hat{x}} \frac{b(y)}{\gamma(y)} \exp\left\{ -\lambda \int_0^y \frac{d\xi}{\gamma(\xi)} \right\} dy < \frac{1}{r},$$

and for $f \in X$ we define

$$H_\lambda(f) := \frac{r}{1 - \alpha_\lambda r} \int_0^{\hat{x}} \frac{f(y)}{\gamma(y)} \exp\left\{ -\lambda \int_0^y \frac{d\xi}{\gamma(\xi)} \right\} dy.$$

Then the solution ϕ of (**) satisfies

$$r\phi(0) = H_\lambda(f).$$

So we get that $\phi \in D$ if $f + H_\lambda(f)b \in D$. We define $V \subseteq X$ as

$$V = \{f \in X: f + H_\lambda(f)b \in D\}.$$

Then $V \subseteq (\lambda - A)D$, and it suffices to show that V is a dense subset of X. Let $f \in X$ and define $g \in X$ as

$$g = f + H_\lambda(f)b.$$

Let $\{g_n\}$ be a sequence in D converging to g as $n \to \infty$. The solution of

$$g_n = f_n + H_\lambda(f_n)b$$

is given by

$$f_n = g_n - \frac{H_\lambda(g_n)}{1 + H_\lambda(b)}\, b.$$

Now $f_n \in V$ and

$$f_n \to g - \frac{H_\lambda(g)}{1 + H_\lambda(b)} \cdot b = f,\ n \to \infty.$$

Therefore $\bar{V} = X$.   □

PROPOSITION 3.4. $A_\varepsilon\phi \to A\phi$ as $\varepsilon \downarrow 0$, for every $\phi \in D$.

Proof. Let $\phi \in D$. Then

$$|(A_\varepsilon\phi)(x) - (A\phi)(x)| \le |b(x)| \cdot \left|\frac{1}{\varepsilon}(\phi(x) - \phi(x - \varepsilon)) - \phi'(x)\right| + r|b(x)| \cdot |\phi(\varepsilon) - \phi(0)|,$$

for every $x \in [0, 1]$, and thus

$$\|A_\varepsilon\phi - A\phi\| = \sup_{x \in [0,1]} |(A_\varepsilon\phi)(x) - (A\phi)(x)| \to 0, \qquad \varepsilon \downarrow 0. \qquad □$$

We are now ready to apply the Trotter-Kato theorem which gives us the following theorem.

THEOREM 3.5. $A \in G(1, \omega)$, and if $\{T(t)\}_{r \ge 0}$ is the semigroup generated by A, then

$$T_\varepsilon(t)\phi \to T(t)\phi, \qquad \varepsilon \downarrow 0,$$

for every $\phi \in X$, where the convergence is uniform for t in bounded subsets of $(0, \infty)$.

This theorem tells us that a solution of the limit equation (3.8) is indeed an approximation of solutions of equation (3.2a), presupposed that their initial condition ϕ is the same.

We can give a very precise description of the relation between the backward and the forward equations and their respective solutions in semigroup terms. It is the backward equation that can be derived rigorously and that is to be solved on the space of continuous functions. Let A_ε be the differential operator on X associated with the backward problem (see (3.2)). Then, by definition, the abstract forward equation is

$$(3.10) \qquad \frac{dn}{dt}(t) = A_\varepsilon^* n(t), \qquad n(0) = \psi \in X^*,$$

where A_ε^*, the dual operator of A_ε, is defined on the dual space $X^* = M[0, 1]$, the space of regular Borel measures on $[0, 1]$. The solutions of (3.10) are given by $n_\varepsilon(t, \cdot\,; \psi) = T_\varepsilon^*(t)\psi$. Here the notion of solution must be understood in terms of the weak* topology on X^*. The dual semigroup $\{T_\varepsilon^*(t)\}_{t \ge 0}$ is a weakly* continuous semigroup with weak* generator A_ε^* (see Butzer and Berens (1967)). There exists the following duality relation between solutions of the forward and the backward equations. For $\phi \in X$ we have

$$(3.11) \qquad \int_0^1 \phi(x)n_\varepsilon(t, dx; \psi) = \langle\phi, n_\varepsilon(t, \cdot\,; \psi)\rangle = \langle\phi, T_\varepsilon^*(t)\psi\rangle$$

$$= \langle T_\varepsilon(t)\phi, \psi\rangle = \langle m_\varepsilon(t, \cdot\,; \phi), \psi\rangle = \int_0^1 m_\varepsilon(t, x; \phi)\psi(dx),$$

where $\langle\,\cdot\,, \cdot\,\rangle$ denotes the duality pairing between X and X^*, and where $m_\varepsilon(t, \cdot\,; \phi)$ is the solution of the backward problem (3.1).

Let $X^\odot$ be the closed subspace of X^* where $\{T_\varepsilon^*(t)\}_{t\geq 0}$ is strongly continuous. Then $X^\odot = \overline{D(A_\varepsilon^*)}$ (see Butzer and Berens (1967)). It can be shown (compare the remark below) that in the present situation $X^\odot = L^1[0, 1]$ (e.g., Clément et al. (1987); (Clément, Heijmans et al. (1987)). Obviously, $X^\odot$ is invariant under $\{T_\varepsilon^*(t)\}_{t\geq 0}$, and the restriction $\{T_\varepsilon^\odot(t)\}_{t\geq 0}$ is a strongly continuous semigroup. If we denote its generator by $A_\varepsilon^\odot$, then

$$\frac{dn}{dt}(t) = A_\varepsilon^\odot n(t), \qquad n(0) = \psi \in X^\odot,$$

is the abstract formulation of (1.4) and with this observation the circle is closed.

Remark. To prove the latter statement, we have to calculate A_ε^* and its domain $D(A_\varepsilon^*)$ from A_ε and $D(A_\varepsilon)$. This calculation involves the following steps (e.g., Heijmans (1984)):

(i) compute the resolvent operator $R(\lambda, A_\varepsilon)$

(ii) compute its dual $R(\lambda, A_\varepsilon^*) = R(\lambda, A_\varepsilon)^*$

(iii) find the domain $D(A_\varepsilon^*)$ from the relation

$$D(A_\varepsilon^*) = \mathrm{Ran}\ (R(\lambda, A_\varepsilon^*)),$$

   $\mathrm{Ran}(\cdot)$ denoting the range

(iv) calculate $A_\varepsilon^* \psi$, where $\psi \in D(A_\varepsilon^*)$, from the relation

$$\langle \phi, A_\varepsilon^* \psi \rangle = \langle A_\varepsilon \phi, \psi \rangle \quad \text{for } \phi \in D(A_\varepsilon)$$

(v) $X^\odot = \overline{D(A_\varepsilon^*)}$ and $A_\varepsilon^\odot$ is the part of A_ε^* in $X^\odot$
   (e.g., Butzer and Berens (1967)).

Our main result of this section, Theorem 3.5, can be restated in terms of solutions of the forward equation by using the duality relation (3.11). We find that for any $\psi \in M[0, 1]$,

$$n_\varepsilon(t, \cdot\,; \psi) \to n(t, \cdot\,; \psi) \quad \text{as } \varepsilon \downarrow 0$$

where convergence holds with respect to the weak* topology of $X^* = M[0, 1]$, and is uniform for t in bounded intervals of $(0, \infty)$.

4. Discussion. In the previous two sections we have proved the essential correctness of two limit arguments initially derived in a heuristic manner. We expect these cases to be exemplary for a general procedure: (i) start imagining how any model simplification works on the level of the individual, (ii) take good care that birth rates keep behaving, (iii) translate individual behavior into a structured population model, both before and after the simplification, (iv) use the Trotter–Kato theorem to connect the two. The upshot from the examples discussed in this paper is that our intuition derived from the individual level appears to be essentially correct when applied to the population level, at least when we are careful. To emphasize the latter point we finish with three cautionary notes.

(i) From a biological point of view the models from which we started in our examples were already fairly metaphorical. In deriving them we made a great number of simplifying assumptions about the underlying biology, comparable to the ones we spelled out in our limit arguments. The nice thing about apparently being able to make our simplifications with impunity already at the level of the individual, is that usually for the more complicated pictures of individual behavior that lie at the start of our considerations we do not even know how to formulate a full population model. Yet, it is of great importance not to be too naive about our simplifications. A thorough analysis of some metaphorical examples such as those we consider in this paper should

help to clarify the issues. In this context we may point to the work of Chipot and Edelstein (1983) on the dynamics of fungal pellet cultures. Their heuristic model formulation basically seems comparable to the formulation that we chose in our second example. Therefore we feel that the limit model embodied in (1.10) also should be the correct model formulation for that particular class of biological systems, and we fail to understand the rationale that led these authors to a different type of equation.

(ii) The Trotter-Kato theorem only gives information about what happens in finite time intervals. Often our main interest is in the long-term behavior of the population model under consideration. Whether the limit argument extends to such properties has to be ascertained in a separate manner. As an example we may refer to Heijmans (1984) who considers both the transient behavior and some properties of the stable i-state distribution (the dominant eigenfunction of the forward equation), as well as the eventual convergence of the p-state towards this distribution, for a model of satiation dependent predatory behavior.

(iii) The proofs in this paper only apply to the linear time-invariant case, i.e., we did not allow any direct or indirect interactions between the individuals. Ultimately, we will wish to extend the limit theorems to the nonlinear case as well. After all, the greatest strength of the structured population methodology is that it allows us for the first time to incorporate various biologically realistic mechanisms for density dependent population regulation, such as a feedback through the limiting of individual growth by food shortage, into analytically formulated population models. Two approaches are possible. Either we could take recourse to direct nonlinear extensions of the Trotter-Kato theorem (compare, e.g., Clément, Heijmans et al. (1987, § 2.3)), or we could try to fall back on the specific mathematical structure of the equations of structured populations, whose main property is that for a given course of the environment the equations are linear (but time-inhomogeneous). Abstractly, such equations take the form

$$(4.1) \qquad \frac{dn}{dt}(t) = A_\varepsilon(E(t))n(t), \qquad n(0) = \phi \in X.$$

Here the vector $E(t)$ describes the environment at time t, and can be calculated as the p-output

$$E(t) = \langle n(t), \xi \rangle$$

for some $\xi \in X^*$. Assuming that, for a given input $E(\cdot)$, the linear time-inhomogeneous equation (4.1) has a solution $n(\cdot)$ we can compute the p-output

$$\tilde{E}(t) = \langle n(t), \xi \rangle.$$

Solving (4.1) amounts to solving the fixed-point equation

$$\tilde{E}(\cdot) = E(\cdot).$$

This fixed-point equation still depends on the parameter ε. If this dependence is continuous (in a sense to be specified) then we might expect that the same is true for its solution.

However, all this is music of a distant future as only the first hesitant steps toward a proof of existence and uniqueness theorems for somewhat more general structured population models of the form (4.1) are being taken at this very moment. Therefore the present paper should only be considered as an introduction to the fascinating problem of putting a more rigorous basis under the structured population methodology.

REFERENCES

P. L. BUTZER AND H. BERENS (1967), *Semigroups of Operators and Approximation*, Springer-Verlag, Berlin, New York.

M. CHIPOT AND L. EDELSTEIN (1983), *A mathematical theory of size distributions in tissue culture*, J. Math. Biol., 16, pp. 115-130.

PH. CLÉMENT, O. DIEKMANN, M. GYLLENBERG, H. J. A. M. HEIJMANS, AND H. R. THIEME (1987), *Perturbation theory for dual semigroups*, I. *The sun-reflexive case*, Math. Ann., 277, pp. 709-725.

PH. CLÉMENT, H. J. A. M. HEIJMANS ET AL. (1987). *One-Parameter Semigroups*, CWI Monographs 5, North-Holland, Amsterdam.

O. DIEKMANN, H. J. A. M. HEIJMANS, AND H. R. THIEME (1984), *On the stability of the cell size distribution*, J. Math. Biol., 19, pp. 227-248.

L. EDELSTEIN AND Y. HADAR (1983), *A model for pellet size distributions in submerged mycelial cultures*, J. Theoret. Biol., 105, pp. 427-452.

H. J. A. M. HEIJMANS (1984), *Holling's 'hungry mantid' model for the invertebrate functional response considered as a Markov process, Part III: Stable satiation distribution*, J. Math. Biol., 21, pp. 115-143.
———— (1986), *Structured populations, linear semigroups, and positivity*, Math. Z., 191, pp. 599-617.

J. A. J. METZ AND O. DIEKMANN (1986), *The Dynamics of Physiologically Structured Populations*, Lecture Notes in Biomathematics 68, Springer-Verlag, Berlin.

J. A. J. METZ, A. M. DE ROOS, AND F. VAN DEN BOSCH (1988), *Population Models Incorporating Physiological Structure*, in Size Structured Populations; Ecology and Evolution, L. Persson and B. Ebenman, eds., Springer-Verlag, Berlin, New York, pp. 106-126.

L. F. MURPHY (1983), *A nonlinear growth mechanism in size structured population dynamics*, J. Theoret. Biol., 104, pp. 493-506.

R. NAGEL, ED. (1986), *One-Parameter Semigroups of Positive Operators*, Lecture Notes in Mathematics, Springer-Verlag, Berlin.

A. PAZY (1983), *Semigroups of Linear Operators and Applications to Partial Differential Equations*, Springer-Verlag, New York.

J. W. SINKO AND W. STRIEFER (1967), *A new model for age-size structure of a population*, Ecology, 48, pp. 910-918.

W. STREIFER (1974), *Realistic models in population ecology*, in Advances in Ecological Research, 8, A. MacFayden, ed., pp. 199-266.

H. F. TROTTER (1958), *Approximation of semigroups of operators*, Pacific J. Math., 8, pp. 887-919.

J. VAN SICKLE (1977), *Analysis of a distributed parameter population model based on physiological age*, J. Theoret. Biol., 64, pp. 571-586.