On the chaotic behaviour of size structured cell populations ☆

S. El Mourchid [a], G. Metafune [b], A. Rhandi [a], J. Voigt [c,*]

[a] *Department of Mathematics, Faculty of Science Semlalia, Cadi Ayyad University, BP 2390, 40000 Marrakesh, Morocco*
[b] *Dipartimento di Matematica "Ennio De Giorgi", Università di Lecce, CP 193, 73100 Lecce, Italy*
[c] *Fachrichtung Mathematik, Technische Universität Dresden, 01062 Dresden, Germany*

Abstract

We show that the solution of a model describing size structured cell populations exhibits chaotic behaviour, for a certain range of parameters. The analysis depends on a uniqueness property in ℓ^2, treated in Appendix A.
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1. Introduction and preliminaries

Our aim is to investigate the chaotic behaviour of a simplified model of a size structured cell population. The model we study is presented in [13]. It is based upon a model developed by Diekmann, Heijmans, and Thieme in [7], studied further by Metz and Diekmann in [14], and analyzed with respect to stability by Greiner and Nagel in [11].

We consider a population of cells described by a function $u(t, x)$ representing the density of cells having size x at time t. We assume that the cells die and divide with death and division rates $\mu(x)$ and $\beta(x)$, respectively, depending on cellular size. Following [13], we additionally include a source term $\nu(x)$ which represents the immigration rate of new cells from a source governed by the density $u(t, x)$. The studied model can be considered to be biologically abnormal insofar as it describes cellular proliferation allowing for arbitrarily small cells. This phenomenon occurs in a disease known as the blood disorder Alpha-thalassemia [12].

For a more detailed discussion of the model we refer to [13,14,17]. With $0 < x < 1$, $t \geqslant 0$, the model has the form

$$\begin{cases} \dfrac{\partial u(t, x)}{\partial t} = -\dfrac{\partial (xu(t, x))}{\partial x} + \gamma(x)u(t, x) - \beta(x)u(t, x) + 4\beta(2x)u(t, 2x)\chi_{(0,\frac{1}{2})}(x), \\ u(0, \cdot) = \phi \in L^1(0, 1). \end{cases} \tag{1.1}$$

Here we have combined the actions of μ and ν in the function $\gamma(x) := \nu(x) - \mu(x)$, which now acts as an excitation rate.

The solution theory of the above model, in the context of the perturbation theory of C_0-semigroups, is described in [13, Section 2]. Under suitable hypotheses, the solution can be obtained in semigroup form

$$u(t, \cdot) := T(t)\phi = \sum_{n=0}^{\infty} T_n(t)\phi,$$

where $T_n(\cdot)$ is defined recursively as

$$\big(T_0(t)\phi\big)(x) := e^{-t} \exp\left(\int_0^t (\gamma - \beta)\big(xe^{-r}\big)\, dr \right) \phi\big(xe^{-t}\big),$$

$$T_{n+1}(t) := \int_0^t T_0(t-s) B T_n(s)\, ds.$$

Here, B is the bounded operator associated with the cellular division process defined as

$$Bu(x) := 4\beta(2x)u(2x)\chi_{(0,\frac{1}{2})}(x).$$

$T_n(\cdot)$ models the growth of the nth generation of cells in our population. (For further biological interpretations we refer to [13].)

Before starting the study of the chaotic behaviour of the above solution, we recall some notions and basic facts related to topological chaos.

Let X be a Banach space, and let $T(\cdot)$ be a C_0-semigroup on X. We say that $T(\cdot)$ is *transitive* if for any two nonempty open subsets U, V of X there exists $t > 0$ such that $(T(t)U) \cap V \neq \emptyset$. $T(\cdot)$ will be called *hypercyclic* provided that there exists $x \in X$, such that $\{T(t)x;\ t \geqslant 0\}$ is dense in X. The following result is proved in [6].

Proposition 1.1. *If X is separable, then the C_0-semigroup $T(\cdot)$ is transitive if and only if it is hypercyclic.*

In order to describe chaotic behaviour we need the following subsets of X:

$$X_0 := \left\{ x \in X;\ \lim_{t \to \infty} T(t)x = 0 \right\},$$

$$X_\infty := \left\{ x \in X;\ \text{for all } \varepsilon > 0 \text{ there exist } y \in X \text{ and } t > 0 \text{ such that } \|y\| < \varepsilon \text{ and } \|T(t)y - x\| < \varepsilon \right\},$$

$$X_p := \left\{ x \in X;\ \text{there exists } t > 0 \text{ such that } T(t)x = x \right\}.$$

In the definition of X_∞, we can take t arbitrarily large. Indeed, let us fix $x \in X_\infty$. For any $n \in \mathbb{N}$, we can find $y_n \in X$ and $t_n > 0$ such that $\|y_n\| < 1/n$ and $\|T(t_n)y_n - x\| < 1/n$. Assume that (t_n) is bounded. Since $T(\cdot)$ is bounded on bounded sets we get $\|T(t_n)y_n\| \to 0$. On the other hand, $\lim_{n \to \infty} T(t_n)y_n = x$. Therefore, if $x \neq 0$, then for each $\varepsilon > 0$, $c > 0$ there exist $y \in X$, $\|y\| < \varepsilon$, and $t > c$ for which $\|T(t)y - x\| < \varepsilon$.

We recall Devaney's definition of chaos (see [3–5]).

Definition 1.2. The C_0-semigroup $T(\cdot)$ is called *chaotic* if it is transitive, and X_p is dense in X.

Desch et al. in [6] give the following sufficient conditions for hypercyclicity using the sets X_0 and X_∞. A similar result can be found in [8].

Theorem 1.3. *If X is separable and X_0, X_∞ are dense then $T(\cdot)$ is hypercyclic. If additionally X_p is dense, then $T(\cdot)$ is chaotic.*

Hereafter we relate the hypercyclicity and chaoticity of a C_0-semigroup to its infinitesimal generator. For C_0-semigroups on Banach spaces, a useful criterion for chaoticity was given in [6], which can be viewed as a continuous

version of the criterion of Godefroy and Shapiro [10]. A C_0-semigroup $T(\cdot)$ generated by a linear operator A in X is chaotic provided that there exists a selection of eigenvectors x_λ of A that is analytic in some open set of the complex plane which meets the imaginary axis, and such that a nondegeneracy condition holds (i.e., a condition for the denseness of eigenvectors). The following recent version of this result is stated in [1].

Theorem 1.4. *Assume that X is separable, and that there exist an open connected subset G of $\mathbb{C}$, $G \subseteq \sigma_p(A)$, and an analytic function $f : G \to X$, satisfying the following conditions*:

(i) $G \cap i\mathbb{R} \neq \emptyset$,
(ii) $f(\lambda) \in \ker(A - \lambda I)$ *for any* $\lambda \in G$,
(iii) *if for some* $\phi \in X^*$ *the function* $\langle \phi, f \rangle$ *is identically zero on G, then $\phi = 0$.*

Then $T(\cdot)$ is chaotic.

The proof of the theorem is based on Theorem 1.3, which makes use of all eigenvalues in G to prove the denseness of the sets X_0, X_∞, and X_p. It turns out that only under some suitable conditions on the purely imaginary point spectrum, $\sigma_p(A) \cap i\mathbb{R}$, the semigroup is hypercyclic (see [2,9]). Theorem 1.4 was successfully applied to prove chaoticity of many systems, ranging from convection-diffusion and transport to birth-and-death and kinetic type equations (see [3,6,15]). Unfortunately, its application to more complicated generators becomes very difficult, if not impossible, especially the verification of condition (iii). For this reason the authors in [1] have investigated the notion of sub-chaoticity. Let us start from a definition.

Definition 1.5. (Cf. [1].) A C_0-semigroup $T(\cdot)$ is called *sub-chaotic* if there exists a closed subspace E which is $T(\cdot)$-invariant, such that the semigroup restricted to E is chaotic. We say that E is a *space of chaoticity* for $T(\cdot)$.

It turns out that the sub-chaoticity is closely related to the first two conditions in Theorem 1.4.

Proposition 1.6. *(Cf. [1].) Suppose that X is separable, and that there exist an open connected subset G of $\mathbb{C}$ and a non-zero analytic function $f : G \to X$ which satisfy conditions* (i) *and* (ii) *of the preceding criterion. Then the semigroup is sub-chaotic, and $V(f, G) := \overline{\text{lin}\{f(\lambda); \ \lambda \in G\}}$ is a space of chaoticity.*

Unfortunately, the space of chaoticity for $T(\cdot)$ given above is not easily evaluated in applications. In some cases, however, this space can be characterized in a more direct way (cf. [1, Criterion 3.8]).

In [13], it was shown that, under certain conditions, each generation of cells described by the family $T_n(\cdot)$ possesses the unstable chaotic behaviour of topological transitivity. What is missing is the proof that the total solution has the same behaviour as well. In the following we will show this up to some simplification of the model. In fact we will assume that the functions $\gamma(\cdot)$ and $\beta(\cdot)$ are constants $\gamma \in \mathbb{R}$ and $\beta \geqslant 0$, respectively.

2. Sub-chaotic and chaotic behaviour

After the simplification, we obtain the model

$$\begin{cases} \dfrac{\partial u(t, x)}{\partial t} = -\dfrac{\partial(xu(t, x))}{\partial x} + \gamma u(t, x) - \beta u(t, x) + 4\beta u(t, 2x)\chi_{(0, \frac{1}{2})}(x), \\ u(0, \cdot) = \phi \in L^1(0, 1). \end{cases}$$

The change of variable $x := e^{-y}$ $(y > 0)$ transforms our model to

$$\begin{cases} \dfrac{\partial v(t, y)}{\partial t} = e^y \dfrac{\partial(e^{-y}v(t, y))}{\partial y} + \gamma v(t, y) - \beta v(t, y) + 4\beta v(t, y - \ln 2)\chi_{(\ln 2, \infty)}(y) =: Av(y), \\ v(0, \cdot) = \psi \in L^1\big((0, \infty), e^{-y} \, dy\big), \end{cases}$$

with $\psi(y) := \phi(e^{-y})$. Expanding the differential term in A one immediately obtains that A is a bounded perturbation of the operator A_0 defined by $A_0 v := \frac{\partial v}{\partial y}$. Therefore the domain of A is given by $D(A) = D(A_0) = \{v \in L^1((0, \infty), e^{-y} \, dy); \ \frac{\partial v}{\partial y} \in L^1((0, \infty), e^{-y} \, dy)\}$.

We recall that A_0 is the generator of the C_0-semigroup of left translations on the weighted space $L^1((0, \infty), e^{-y}\, dy)$, which is hypercyclic by [6, Theorem 4.7]. This corresponds to the parameters $\gamma = 1$, $\beta = 0$. We will show below that this semigroup is even chaotic.

Proposition 2.1. *If $\gamma - 3\beta > 0$ then the C_0-semigroup generated by A is sub-chaotic on $L^1((0, \infty), e^{-y}\, dy)$.*

Proof. Let v_λ be an eigenfunction of the operator A, associated with the eigenvalue λ. Denoting by v^n the restriction of v_λ to the interval $(n \ln 2, (n + 1) \ln 2)$, the sequence $(v^n)_{n=0}^\infty$ satisfies

$$
\begin{cases}
v^0(y) = e^{(\lambda - \eta)y}, & \text{for } 0 < y < \ln 2, \\
(v^n)'(y) = (\lambda - \eta)v^n - 4\beta v^{n-1}(y - \ln 2), & \text{for } n \ln 2 < y < (n + 1) \ln 2, \ n \geqslant 1,
\end{cases}
$$

where we have used the abbreviation $\eta := \gamma - \beta - 1$. Solving this system of equations by induction and taking into account that the function v_λ is continuous at $n \ln 2$ $(n \geqslant 1)$ we obtain

$$
v_\lambda(y) = e^{(\lambda - \eta)y} \sum_{n=0}^\infty \frac{(-4\beta e^{-(\lambda - \eta)\ln 2})^n}{n!} (y - n \ln 2)^n \chi_{(n \ln 2, \infty)}(y).
$$

The function v_λ belongs to $L^1((0, \infty), e^{-y}\, dy)$ provided that $\operatorname{Re} \lambda < \eta + 1 - 2\beta = \gamma - 3\beta$, as shown by the following estimate:

$$
\int_0^\infty |v_\lambda(y)| e^{-y}\, dy \leqslant \sum_{n=0}^\infty \int_{n \ln 2}^\infty e^{(\operatorname{Re} \lambda - \eta)y} \frac{(4\beta e^{-(\operatorname{Re} \lambda - \eta)\ln 2})^n}{n!} (y - n \ln 2)^n e^{-y}\, dy
$$

$$
= \sum_{n=0}^\infty \int_0^\infty e^{(\operatorname{Re} \lambda - \eta)(y + n \ln 2)} \frac{(4\beta e^{-(\operatorname{Re} \lambda - \eta)\ln 2})^n}{n!} y^n e^{-n \ln 2} e^{-y}\, dy
$$

$$
= \int_0^\infty e^{(\operatorname{Re} \lambda - \eta)y} e^{-y} \sum_{n=0}^\infty \frac{(4\beta y)^n}{n!} 2^{-n}\, dy = \int_0^\infty e^{(\operatorname{Re} \lambda - \eta - 1 + 2\beta)y}\, dy.
$$

Thus the point spectrum $\sigma_p(A)$ contains the left half plane $G := \{\lambda \in \mathbb{C};\ \operatorname{Re} \lambda < \gamma - 3\beta\}$ which intersects the imaginary axis provided that $\gamma - 3\beta > 0$. Now, we prove that our choice of the eigenfunctions yields a weakly analytic function $\lambda \mapsto v_\lambda$ on G, which, in turn, is equivalent to analyticity. For this let $\phi \in L^\infty(0, \infty)$. As in the preceding estimate one has $|y \mapsto e^{-y}\phi(y) v_\lambda(y)| \leqslant \|\phi\|_\infty (y \mapsto e^{(\operatorname{Re} \lambda - \gamma + 3\beta)y}) \in L^1(0, \infty)$, for every $\lambda \in G$. Using the dominated convergence theorem, we obtain

$$
\int_0^\infty \phi(y) v_\lambda(y) e^{-y}\, dy = \sum_{n=0}^\infty \int_{n \ln 2}^\infty \phi(y) e^{(\lambda - \eta)y} \frac{(-4\beta e^{-(\lambda - \eta)\ln 2})^n}{n!} (y - n \ln 2)^n e^{-y}\, dy
$$

$$
= \sum_{n=0}^\infty \int_0^\infty \phi(y + n \ln 2) e^{(\lambda - \eta)(y + n \ln 2)} \frac{(-4\beta e^{-(\lambda - \eta)\ln 2})^n}{n!} y^n e^{-n \ln 2} e^{-y}\, dy
$$

$$
= \int_0^\infty e^{(\lambda - \eta)y} e^{-y} \sum_{n=0}^\infty \phi(y + n \ln 2) \frac{(-4\beta y)^n}{n!} 2^{-n}\, dy = \int_0^\infty e^{\lambda y} \psi(y)\, dy,
$$

where $\psi(y) := e^{-(\gamma - \beta)y} \sum_{n=0}^\infty \phi(y + n \ln 2) \frac{(-2\beta y)^n}{n!}$, for $y > 0$, is exponentially bounded, $|\psi(y)| \leqslant \|\phi\|_\infty e^{(3\beta - \gamma)y}$. This shows that the function $\lambda \mapsto \langle \phi, v_\lambda \rangle$ defined on G is the reflected Laplace transform of ψ, and therefore is analytic on G. Using Proposition 1.6, we deduce that the semigroup generated by A is sub-chaotic. $\quad\square$

The following result is a consequence of the analysis presented in Appendix A.

Proposition 2.2. *Assume that $\gamma - 3\beta > 0$, and let G and v_λ be as defined in the proof of Proposition 2.1.*

(a) *Let $0 \leqslant \beta \leqslant \frac{1}{2\ln 2}$. Let $\phi \in L^\infty(0, \infty)$ be such that $\langle \phi, v_\lambda \rangle = 0$ for all $\lambda \in G$. Then $\phi = 0$.*
(b) *Let $\beta > \frac{1}{2\ln 2}$. Then there exists $\phi \in L^\infty(0, \infty)$, $\phi \neq 0$, such that $\langle \phi, v_\lambda \rangle = 0$ for all $\lambda \in G$.*

Proof. Let $\phi \in L^\infty(0, \infty)$. By the injectivity of the Laplace transformation we obtain that $\langle \phi, v_\lambda \rangle = 0$ on G if and only if

$$\sum_{n=0}^{\infty} \phi(y + n\ln 2)\frac{(-2\beta y)^n}{n!} = 0 \quad \text{a.e. on } (0, \infty). \tag{2.1}$$

For the function $\psi \in L^\infty(0, \infty)$ defined by $\psi(x) = \phi(x\ln 2)$, Eq. (2.1) is equivalent to

$$\sum_{n=0}^{\infty} \psi(x + n)\frac{(-2\beta x\ln 2)^n}{n!} = 0 \quad \text{a.e. on } (0, \infty). \tag{2.2}$$

(a) For $\beta = 0$, the sum in (2.1) reduces to the 0th term, and one concludes $\phi(y) = 0$ a.e. It remains to treat the case $\beta > 0$.

We define ψ as above and choose a bounded measurable representative of ψ (still called ψ). There exists a null set $N \subseteq (0, 1]$ such that

$$\sum_{n=0}^{\infty} \psi(x + n)\frac{(-2\beta x\ln 2)^n}{n!} = 0 \tag{2.3}$$

holds for all $x \in (0, \infty) \setminus \bigcup_{n \in \mathbb{N}_0}(N + n)$. Then, for $x \in (0, 1] \setminus N$, the sequence $a := (\psi(x+n))_{n=0}^{\infty} \in \ell^\infty$ is a sequence satisfying the hypotheses of Corollary A.3 or A.4, with $-1 \leqslant \alpha := -2\beta\ln 2 < 0$. Thus, it follows from Corollary A.3 or A.4 that $a = 0$. This shows $\psi(x) = 0$ for all $x \in (0, \infty) \setminus \bigcup_{n \in \mathbb{N}_0}(N + n)$.

(b) If $\beta > \frac{1}{2\ln 2}$, then the function ψ defined by

$$\psi(x) := x\left(\frac{1}{2\beta\ln 2}\right)^x, \quad \text{for } x > 0,$$

is in $L^\infty(0, \infty)$ and satisfies (2.3). Hence, the assertion follows by taking

$$\phi(y) := \frac{y}{\ln 2}\left(\frac{1}{2\beta\ln 2}\right)^{\frac{y}{\ln 2}}, \quad \text{for } y > 0. \qquad \square$$

Now, using Propositions 2.1 and 1.6 we deduce the main result of this paper.

Theorem 2.3. *Let $\gamma - 3\beta > 0$. Then A generates a sub-chaotic C_0-semigroup, where $Y := \overline{\ln\{v_\lambda; \ \operatorname{Re}\lambda < \gamma - 3\beta\}}$ is a space of chaoticity. One has $Y = L^1((0, \infty), e^{-y}\, dy)$ if and only if $0 \leqslant \beta \leqslant \frac{1}{2\ln 2}$, and in this case the semigroup generated by A is chaotic.*

Appendix A

In this appendix we analyze whether, for given $x > 0$, $\alpha \in \mathbb{R} \setminus \{0\}$, the discrete problem

$$\sum_{n=0}^{\infty} a_{n+k}\frac{(\alpha(x+k))^n}{n!} = 0, \quad \text{for all } k \in \mathbb{N}_0, \tag{A.1}$$

has a non-trivial solution $(a_n) \in \ell^\infty$.

We start with the observation that the sequence (a_n), given by $a_n := (x + n)(-\frac{1}{\alpha})^n$, is a solution of (A.1). Thus, for $|\alpha| > 1$, we have found a solution $(a_n) \in \ell^2 \subseteq \ell^\infty$.

The essential part of the analysis of the problem is contained in the following uniqueness result. (The result expresses the fact that a certain sequence of elements in ℓ^2 is total.)

Proposition A.1. *Let $x > 0$, $a = (a_n) \in \ell^2$, and assume that*

$$\sum_{n=0}^{\infty} a_{n+k} \frac{(x+k)^n}{n!} = 0, \quad \text{for all } k \in \mathbb{N}_0. \tag{A.2}$$

Then $a = 0$.

In the proof of Proposition A.1 we will use the Hardy space

$$H^2(D) = \left\{ f \in H(D); \; \|f\|_2 := \sup_{r<1} \left(\frac{1}{2\pi} \int_0^{2\pi} |f(re^{i\theta})|^2 \, d\theta \right)^{\frac{1}{2}} < \infty \right\},$$

where $D := \{z \in \mathbb{C}; \; |z| < 1\}$, and where $H(D)$ denotes the space of all holomorphic functions in D. We recall that

$$\|f\|_2^2 = \sum_{n=0}^{\infty} |a_n|^2 \quad \text{if } f(z) = \sum_{n=0}^{\infty} a_n z^n.$$

We start with a preparation for the proof.

Lemma A.2. *The space $\lin\{(ze^z)^k; \; k \in \mathbb{N}_0\}$ is dense in $H(D) \cap C(\overline{D})$, with respect to the supremum norm.*

Proof. Defining $J(z) = ze^z$, it is not too difficult to verify that $J: D \to \Omega$, where $\Omega = J(D)$, is biholomorphic, and that $J: \overline{D} \to \overline{\Omega}$ is a homeomorphism.

Let $\phi \in H(D) \cap C(\overline{D})$. Then $\phi \circ J^{-1} \in H(\Omega) \cap C(\overline{\Omega})$. By Mergelyan's theorem (see, e.g., [16, Theorem 20.5]) there exists a sequence (p_n) of polynomials such that

$$p_n \to \phi \circ J^{-1}, \quad \text{uniformly on } \overline{\Omega},$$

and this implies

$$p_n \circ J \to \phi, \quad \text{uniformly on } \overline{D}.$$

Since $p_n \circ J$ are polynomials in ze^z we obtain the assertion. $\quad \square$

Proof of Proposition A.1. Let $h(z) := \sum_{n=0}^{\infty} a_n z^n$. For $k \in \mathbb{N}_0$ we compute

$$e^{xz}(ze^z)^k = z^k e^{(x+k)z} = \sum_{n=0}^{\infty} (x+k)^n \frac{z^{n+k}}{n!} = \sum_{n=k}^{\infty} (x+k)^{n-k} \frac{z^n}{(n-k)!}.$$

This implies

$$\langle h, e^{xz}(ze^z)^k \rangle_{H^2} = \sum_{n=k}^{\infty} a_n \frac{(x+k)^{n-k}}{(n-k)!} = \sum_{n=0}^{\infty} a_{n+k} \frac{(x+k)^n}{n!} = 0,$$

and thus $h \perp e^{xz}(ze^z)^k$, for all $k \in \mathbb{N}_0$.

Since $H(D) \cap C(\overline{D})$ is dense in $H^2(D)$, Lemma A.2 implies that $\lin\{(ze^z)^k; \; k \in \mathbb{N}_0\}$ is dense in $H^2(D)$. The mapping $H^2(D) \ni f \mapsto e^{xz} f \in H^2(D)$ is an isomorphism (of Banach spaces), and therefore $\lin\{e^{xz}(ze^z)^k; \; k \in \mathbb{N}_0\}$ is dense in $H^2(D)$ as well. Since h is orthogonal to this set we conclude that $h = 0$. $\quad \square$

Corollary A.3. *Let $x > 0$, $\alpha \in \mathbb{R}$, $0 < |\alpha| < 1$, $a = (a_n) \in \ell^\infty$, and assume that* (A.1) *is satisfied. Then $a = 0$.*

Proof. The sequence $(\alpha^n a_n)_n$ belongs to ℓ^2 and is a solution of (A.2). Therefore Proposition A.1 implies $(\alpha^n a_n)_n = 0$. $\quad \square$

Corollary A.4. *Let $x > 0$, $\alpha = \pm 1$, $a = (a_n) \in \ell^\infty$, and assume that a is a solution of* (A.1). *Then $a = 0$.*

Proof. Replacing a by $((-1)^n a_n)$, if $\alpha = -1$, we may assume that a is a solution of (A.2).

Setting $b_n = \frac{a_n}{x+n}$ ($n \in \mathbb{N}_0$), we obtain $(b_n)_n \in \ell^2$, and (A.2) implies

$$0 = \sum_{n=0}^{\infty} (x + n + k) b_{n+k} \frac{(x+k)^n}{n!} = (x+k) \sum_{n=0}^{\infty} (b_{n+k} + b_{n+k+1}) \frac{(x+k)^n}{n!},$$

which in turn implies

$$\sum_{n=0}^{\infty} (b_{n+k} + b_{n+k+1}) \frac{(x+k)^n}{n!} = 0, \quad \text{for all } k \in \mathbb{N}_0.$$

This is equivalent to

$$\sum_{n=0}^{\infty} \big((I+L)b\big)_{n+k} \frac{(x+k)^n}{n!} = 0, \quad \text{for all } k \in \mathbb{N}_0,$$

where L denotes the left shift on ℓ^2. This means that $(I+L)b \in \ell^2$ satisfies (A.2), and therefore Proposition A.1 shows $(I+L)b = 0$. It is standard (and easy to show) that -1 is not an eigenvalue of L, and therefore $b = 0$. $\quad\square$

Acknowledgments

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