# Asymptotic behavior and effective boundaries for age-structured population models in a periodically changing environment

Department of Mathematics, Linköping University

**Jonathan Andersson**

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| Credits: | **30 hp** |
| Level: | **A** |
| Supervisor: | **Bengt-Ove Turesson**,<br>Department of Mathematics, Linköping University |
| Examiner: | **Vladimir Kozlov**,<br>Department of Mathematics, Linköping University |
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# Abstract

Human activity and other events can cause environmental changes to the habitat of organisms. The environmental changes effect the vital rates for a population. In order to predict the impact of these environmental changes on populations, we use two different models for population dynamics. One simpler linear model that ignores environmental competition between individuals and another model that does not. Our population models take into consideration the age distribution of the population and thus takes into consideration the impact of demographics. This thesis generalize two theorems, one for each model, developed by Sonja Radosavljevic regarding long term upper and lower bounds of a population with periodic birth rate ; see [6] and [5]. The generalisation consist in including the case where the periodic part of the birth rate can be expressed with a finite Fourier series and also infinite Fourier series under some constraints. The old theorems only considers the case when the periodic part of the birth rate can be expressed with one cosine term. From the theorems we discover a connection between the frequency of oscillation and the effect on population growth. From this derived connection we conclude that periodical changing environments can have both positive and negative effects on the population.

**Keywords:**

age-structure, time-dependency, environmental variability, upper and lower boundaries, periodic oscillations, logistic

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# Nomenclature

| | |
|---|---|
| $\mu$ | Death rate function |
| $a$ | Age-variable |
| $f$ | Initial age distribution function |
| $m$ | Birth rate function |
| $N$ | Population size |
| $n$ | Age distribution |
| $t$ | Time-variable |

# Contents

# Chapter 1

# Background population dynamics

In this chapter we give a short introduction to the subject of population dynamics. Different models for population growth will be presented. The underlying difference between the population models is which natural factors that are considered in the model. The more factors that are included in the model the more complex and harder the model becomes to analyse.

Population dynamics is the study of population sizes and age composition as dynamical systems. There are many ways to model populations. The modeler are in many cases faced with the decision of making realistic or easy to use models. There are a variety of things to consider when deciding on how to model population growth.

One useful simplification of a population that is often used is to make the population size a continuous function despite that the number of individuals in a population has to be an integer. Because the number of individuals in a population is often large and continuous models are easy to analyse, continuous models are often preferred when dealing with population dynamics. We will continue to use this simplification.

Two central parts for every model is the vital rates: the birth rate and the death rate. The birth rate is a measurement of how many births a population produces compared to its size at a given time. It represents the population growth rate relative to the size of the population in a population with no deaths and no net migration. Such a population may be modeled by the following equation:

$$N'(t) = mN(t) \quad \text{for } t > 0$$

where $m$ is the birth rate and $N$ is the population size. In a similar way, the death rate $\mu$ is the number that represents the growth rate of a population without birth rate and no net migration. Such a population may be modeled by the following equation:

$$N_t' = -\mu N \quad \text{for } t > 0.$$

In the more general case when both death rate and birth rate are nonzero we have that

$$N'(t) = (m - \mu)N(t) \quad \text{for } t > 0.$$

As mentioned earlier there are many different population models. The primary thing that makes the models different is how the vital rates are modeled. The simplest model is when the vital rates are considered to be constant, but the cases where a population can be modeled with constant vital rates are rare.

In nature vital rates changes with time. This can be due to seasonal changes or other reasons such as pollution. If we consider the case where the vital rates are time dependent we get the equation

$$N'(t) = (m(t) - \mu(t))N(t) \quad \text{for } t > 0$$

which is called the balance equation and has the general solution

$$N(t) = Ce^{-\int_0^t m(\tau)-\mu(\tau)d\tau},$$

where $C$ is a constant that can be determined by the initial condition $N(0) = N_0$ that gives $C = N_0$. If we consider the case with no birth rate we have that

$$N(t) = N_0 e^{-\int_0^t \mu(\tau)d\tau}.$$

From this we can deduce that the chance of a living specimen at time $t_0$ surviving a time period $t$ is

$$\frac{N(t+t_0)}{N(t_0)} = e^{-\int_{t_0}^{t_0+t} \mu(\tau)d\tau}.$$

It is often convenient to only take into consideration the females of a population. In that case we can for example get a clear definition with what we mean by the chance of an individual to give birth at time $t$. That would be the chance of an individual to give birth to a female. Since males can impregnate several females relatively cost free, the total population does not get largely effected by moderate changes in the male population; see [4].

There is more things that the vital rates are dependent of and that can be modeled. Examples of this are age, predators, statuses like pregnancy and sickness, position and delay effects.

Age can be a factor that needs to be taken into consideration. The age is important when it is believed that the age structure of the population is going to change. In nature age is always something that impacts the vital rates. If the demographics are not believed to change, one can ignore the age composition and simply use vital rates average for the whole population.

When taking age into account, we are not only interested in the total size of a population but also how many individuals there are of a certain age. This gives reason to introduce a population density function $n(a,t)$ dependent on time $t$ satisfying that the number of individuals older than a certain age, say $a_1$, and younger than an age $a_2$ at time $t$ is given by

$$\int_{a_1}^{a_2} n(a,t)da \quad \text{for } t > 0.$$

Thus the whole population $N(t)$ is given by

$$N(t) = \int_{0}^{\infty} n(a,t)da \quad \text{for } t > 0.$$

Since we in later chapters will deal with two different age structured models we will leave the details of age structured models for later.

The vital rates for certain species $A$ can depend on the population size of other species $B_1, B_2, B_3, \ldots$ The most obvious example is the number of predators and preys that exist in the same habitat. Other examples are the number of pollinators, symbiotic species and competing species in the habitat. The population size of $B_1, B_2, B_3, \ldots$ in turn can be dependent on other species including $A$ which gives rise to large differential systems.

Let us consider the case where we have two interacting species $U$ and $V$ where $U$ is prey and $V$ is predator. One simple example of a balance equation is

$$\begin{cases} U' = \alpha U - \gamma UV \\ V' = e\gamma UV - \beta V \end{cases}$$

where the parameters of $\alpha$, $\beta$, $\gamma$ and $e$ are all positive.

In some situations it can be necessary to introduce statuses in a model. During its lifetime an individual can achieve different stage. The individual can become pregnant, infected by a disease or pass through intermediate stages during its life such as being a larvea, tadpool or cocon.

In many cases a population moves between different habitats. To model the effects of a moving population, we have to make the vital rates position dependent. Similarly to the age structured model we have to introduce an spatial density function $n(a,t,x)$, $x \in \mathbb{R}^2$ for the population. Movement within a species are especially interesting when studying the effect of transmittable diseases. In order to simplify the model the landscape is usually divided into a set of many patches; see [3].

# Chapter 2

# Linear age-structured population model

## 2.1 Introduction

Due to technological breakthroughs the human species has thrived at the expanse of many other species. Human activity causes environmental change, pollution, destruction and reduction of natural habitats. This have caused many species to become endangered or extinct. In order to foresee and prevent extinctions it is important to understand population dynamics.

Ignoring migration which will not be taken into consideration, the birth and death rate are the two factors that impacts population growth. For small populations, demographics is an important factor and since our research is foremost meant to study populations that faces extinction it is necessary to model the vital rates as age dependent. We also suppose hat the vital rates are changing with time. There are many different models for population growth but we will focus on two specific models. The first model we will use is a slightly modified version of the population model that was developed by McKendrick and von Foerster; see [2]. The McKendrick -von Foerster model has the great advantage of being linear and easy to analyse. Since it takes into consideration that the death rate and the birth rate depend on the individuals age it is useful when the demographics plays an important role. On the other hand, von Foerster's model has the weakness of ignoring boundaries of the populations habitat, which would have prevented the population from growing forever and become infinitely large. Usually the population size will either converge to $\infty$ or 0 when the time goes toward infinity. The same applies to our modified model.

We are interested in the effects of demographics and want to study the effects of vital rates that are periodic in time. taking this into consideration we will use the population model developed by von Foerster and generalise it by making the vital rates time dependent. We have the following balance equation:

$$\frac{\partial n(a,t)}{\partial t} + \frac{\partial n(a,t)}{\partial a} = -\mu(a,t)n(a,t), \quad a,t > 0 \tag{2.1}$$

and the boundary and initial conditions are given by

$$n(0,t) = \int_0^\infty m(a,t)n(a,t)da, \quad t > 0 \tag{2.2}$$

$$n(a,0) = f(a), \quad a \geq 0 \tag{2.3}$$

where $n_t(a) = n(a,t)$ represent the age distribution of the population at time $t$, the death rate and birth rate are age and time dependent and denoted $\mu(a,t)$ and $m(a,t)$ respectively and $f(a)$ is the initial age distribution of the population.

We assume that there is an upper bound on the age of individuals and denote this bound by $A_\mu$. The individuals in a population also have a constant lower and upper bound on the fertile phase of individuals. We assume that the functions $m(a,t), \mu(a,t)$ and $f(a)$ satisfies the following properties:

(i) $m(a,t)$ is bounded for $a,t \geq 0$
$m(a,t) = 0$ for $a > A_\mu$ and $t \geq 0$
$m(a,t) \geq \delta_1 > 0$ for $a_1 < a < a_2$, where $0 < a_1 < a_2 < A_\mu$ and $t \geq 0$

(ii) $0 < c_\mu \leq \mu(a,t) \leq C_\mu < \infty$ for $t \geq 0$ and $t \geq 0$
$\int_A^{A+A_\mu} \mu(a,t)da = \infty$ for $t \geq 0$ and $A \geq 0$

(iii) $f$ is bounded
$f(a) \geq \delta_2 > 0$ for $0 < a < a_2$
$f(a) = 0$ for $a > A_\mu$

The balance equation (2.1) can be best understood by doing a linear parameterisation of the variabels as $a = x$ and $t = x + c$, where $c$ is a constant. Doing this and using the chain rule, (2.1) becomes

$$\frac{\partial n(x,x+c)}{\partial x} = -\mu(x,x+c)n(x,x+c), \quad \text{for } c > -x \tag{2.4}$$

If we let $c = t - a$ we can read from (2.4) that the size of the sub-population of individuals that has a certain age $a$ at a certain time $t$ drops with time during a short time period $dt$ by $\mu(a,t)n(a,t)dt$

The parametrisation also makes it possible to solve the equation for constant $\mu$. Even if we are not interested in a solution for constant $\mu$ we can still use the same method to produce an alternative expression for $n(a,t)$. This was done by Radosavljevic in [6].

**Theorem 2.1.1.** *Let $n(a,t)$ be a solution to (2.1) with boundary and initial condition (2.2) and (2.3). Then*

$$\begin{aligned} n(0,t) &= \int_0^t m(a,t)e^{-\int_0^a \mu(v,v+t-a)dv} n(0,t-a)da \\ &\quad + \int_t^\infty m(a,t)e^{-\int_{a-t}^a \mu(v,v+t-a)dv} f(a-t)da \end{aligned} \tag{2.5}$$

*for $t > 0$. For $a > 0$, $n(a,t)$ is given by*

$$n(a,t) = \begin{cases} n(0,t-a)e^{-\int_0^a \mu(v,v+t-a)dv}, & a < t \\ f(a-t)e^{-\int_{a-t}^a \mu(v,v+t-a)dv}, & a \geq t \end{cases}. \tag{2.6}$$

Equation (2.5) can be written in the following way:

$$n(0,t) = Kn(0,t) + Ff(t) = Gn(0,t), \quad t \geq 0 \tag{2.7}$$

where

$$Kn(0,t) = \int_0^t m(a,t)e^{-\int_0^a \mu(v,v+t-a)dv} n(0,t-a)da, \quad t \geq 0$$

and

$$Ff(t) = \int_t^\infty m(a,t)e^{-\int_{a-t}^a \mu(v,v+a-t)dv} f(a-t)da, \quad t \geq 0.$$

*Proof.* We have from equation (2.4) that if

$$n(x, x+c) = Z(x),$$

then we have that

$$\frac{\partial Z(x)}{\partial x} = -\mu(x, x+c)Z(x), \text{ for } c > -x$$

which has the solution

$$Z(x) = Z(0)e^{-\int_0^x \mu(v,v+c)dv}.$$

Expressed in terms of $n$ we get

$$n(x, x+c) = \begin{cases} n(0, c)e^{-\int_0^x \mu(v,v+c)dv}, & c > 0 \\ n(-c, 0)e^{-\int_{-c}^x \mu(v,v+c)dv}, & c \leq 0 \end{cases}.$$

Given that $a = x$, $t = x + c$ and $n(a, 0) = f(a)$, we get that

$$n(a,t) = \begin{cases} n(0, t-a)e^{-\int_0^a \mu(v,v+t-a)dv}, & t > a \\ f(a-t)e^{-\int_{a-t}^a \mu(v,v+t-a)dv}, & t \leq a \end{cases}.$$

From equation (2.5) we now get

$$\begin{aligned} n(0,t) = &\int_0^t m(a,t)e^{-\int_0^a \mu(v,v+t-a)dv} n(0, t-a)da \\ &+ \int_t^\infty m(a,t)e^{-\int_{a-t}^a \mu(v,v+t-a)dv} f(a-t)da, \quad t > 0. \end{aligned}$$

□

At first the equations (2.5) and (2.6) might seem quite daunting but with a few observations we can find a simple meaning to it.

First if we look at equation (2.6) we see that $n(a, t)$ the number of individuals aged $a$ at time $t$ is the product of how many was born at time $(t - a)$ that is $n(0, t - a)$ or $f(a - t)$ (depending on if $a > t$) and a factor that has to be the ratio of those born at $(t - a)$ that survives until they are at least aged $a$ which apparently from equation (2.5) is $e^{-\int_0^a \mu(v,v+t-a)dv}$. The factor $e^{-\int_0^a \mu(v,v+t-a)dv}$ can thus be interpreted as the probability of an individual born at time $(a - t)$ to reach age $a$. In the appendix there is an alternative way of deriving the interpretation of $e^{-\int_0^a \mu(v,v+t-a)dv}$.

Now if we look at the renewal equation (2.5) we see that the numbers of newborns at time $t$ is the sum of the product of the number of survivors from each generation and their birth rate at time $t$, as we would expect intuitively.

For brevity we use the notation

$$Q(a,t) = m(a,t)e^{-\int_0^a \mu(v,v+t-a)dv}, \quad a \geq 0,\, t \geq 0. \tag{2.8}$$

We can interpret $Q(a, t)$ as the birth rate of individuals aged $a$ at time $t$ including those that have already died. To clarify we simply imagine that we include those individuals that have died before the age of $a$ but would, if they lived, have been of age $a$ at time $t$ into the population and rightly assume that the dead has zero birth rate. We can denote $Q(a, t)$ as the "dead including birth rate".

We will now look at how to prove existence and uniqueness of solutions for equation (2.5). For this we need the Banach's fixed point theorem.

**Definition 2.1.1.** . Suppose that $(X, d)$ is a metric space and $F$ is a mapping from $X$ to $X$. The mapping $F$ is called a contraction mapping if there exists a constant $0 \leq L < 1$ such that $d(F(x), F(y)) \leq Ld(x, y)$ for all $x, y \in X$.

**Theorem 2.1.2** (Banach's Fixed Point Theorem). *Suppose $X$ is a complete metric space. Then every contraction $F : X \to X$ has a uniquely determined fixed point.*

We denote $L^\infty_\Lambda(0, \infty)$ the space of measurable functions u on $[0, \infty)$ that satisfy $|u(t)|= O(e^{\Lambda t})$ for $t \geq 0$ where $\Lambda$ is a positive real number. The norm $||u||_\Lambda$ on $L^\infty_\Lambda(0, \infty)$ is defined by

$$||u||_\Lambda = \sup_{t>0} |u(t)|e^{-\Lambda t}.$$

**Lemma 2.1.3.** *[6] The operator $G$ is a contraction on $L^\infty_\Lambda(0, \infty)$ if $\Lambda$ is sufficiently large.*

With the aid of Lemma 2.1.3 and Banach's fixed point theorem deduce that the renewal equation (2.7) has a unique solution. Even though von Foersters equation is linear, it can be hard to solve analytically. When solving von Foersters equation numerically, the standard way is to express it in the form of equation (2.7) and use the fact that the sequence $(n_k)^\infty_{k=0}$ defined by

$$n_{k+1} = Kn_k + Ff, \quad n_0 = 0, \quad k = 0, 1, \ldots$$

converges to the solution $n$. Furthermore we have that the sequence converges to $n$ no matter what $n_0$ is. We can easily see that the sequence $(n_k)^\infty_{k=0}$ is non-negative, so the solution has to be non-negative. The iterative way to approximate $n$ does not work when we want to study the behavior of $n$ for large $t$. We will instead use the theory of upper and lower solution to approximate $n(0, t)$ for large $t$ and thereby as we will see the total population.

## 2.2 General upper and lower bounds

Finding an analytical solution to (2.1)-(2.3) is usually impossible. We are interested in finding lower and upper bounds of the solution $n(a, t)$ for large $t$. For this we can use equation (2.7) and the theory of upper and lower solution. A more thorough analysis on the theory of upper and lower solution can be found in Section 7.4 in [1].

**Definition 2.2.1.** A non-negative function $n_+ \in L^\infty_\Lambda(0, \infty)$ is an upper solution to equation (2.7) if

$$n_+(t) \geq Kn_+(t) + F(f(t)), \quad \text{for } t > 0.$$

Similarly a non-negative function $n_- \in L^\infty_\Lambda(0,\infty)$ is a lower solution to equation (2.7) if

$$n_-(t) \le Kn_-(t) + Ff(t), \quad \text{for } t > 0.$$

The upper and lower solution are important because they define upper and lower bounds of $n(0,t)$, that is

$$n_-(t) \le n(0,t) \le n_+(t), \quad \text{for } t > 0. \tag{2.9}$$

To see why the inequalities (2.9) hold we first note that the operator $G$ is a monotonically increasing operator meaning that if $n_1(t) \le n_2(t)$ for every $t$ then $G(n_1(t)) \le G(n_2(t))$ for all $t$. Now we introduce the sequence $(n_k)_{k=0}^\infty$ defined by

$$n_{k+1} = G(n_k), \quad n_0 = n^+, \quad k = 0, 1, .....$$

where $n^+$ is an upper solution. Since $n^+$ is an upper solution we have that

$$G(n_0) \le n_0$$

and since $G$ is monotone and because the iterative sequence converges to the solution $n$ we have that

$$n^+ = n_0 \ge G(n_0) = n_1 \ge G(n_1) \ge .... \ge n.$$

In a similar way we can prove that $n^- \le n$.

In [6] Radosavljevic uses the theory of upper and lower solution to prove the following theorem:

**Theorem 2.2.1.** *Suppose that $M \ge A_\mu$ and let $n$ be a solution to equation (2.7). If the function $\sigma \in L^\infty(0,\infty)$ satisfies*

$$\int_0^\infty Q(a,t)e^{-\int_{t-a}^t \sigma(\tau)d\tau} da \le 1, \quad t \ge M$$

*then there exist a $D > 0$ such that*

$$n(0,t) \le De^{\int_0^t \sigma(\tau)d\tau}, \quad t \ge M.$$

**Theorem 2.2.2.** *Suppose that $M \ge A_\mu$ and let $n$ be a solution to equation (2.7). If the function $\sigma \in L^\infty(0,\infty)$ satisfies*

$$\int_0^\infty Q(a,t)e^{-\int_{t-a}^t \sigma(\tau)d\tau} da \ge 1, \quad t \ge M$$

*then there exist a constant $C > 0$ such that*

$$n(0,t) \ge Ce^{\int_0^t \sigma(\tau)d\tau}, \quad t \ge M.$$

In particular we get the following theorem from Theorem 2.2.2 and Theorem 2.2.1:

**Theorem 2.2.3.** *Suppose that $M \geq A_\mu$. If the function $\sigma \in L^\infty(0,\infty)$ satisfies*

$$\int_0^\infty Q(a,t)e^{-\int_{t-a}^t \sigma(\tau)d\tau}da = 1, \quad t \geq M \tag{2.10}$$

*then there exist constants $C$ and $D$ such that*

$$Ce^{\int_0^t \sigma(\tau)d\tau} \leq n(0,t) \leq De^{\int_0^t \sigma(\tau)d\tau},\ t \geq M.$$

Upper and lower bounds of $n(0,t)$ are important because they provide upper and lower bounds of the whole population. The total population is defined by

$$N(t) = \int_0^\infty n(a,t)da, \quad t \geq 0.$$

**Theorem 2.2.4.** *If $\sigma \in L^\infty(0,\infty)$ satisfies*

$$\int_0^\infty Q(a,t)e^{-\int_{t-a}^t \sigma(\tau)d\tau}da = 1, \quad t \geq M.$$

*where $M \geq A_\mu$, then there exist two positive constants $C$ and $D$ such that*

$$Ce^{\int_0^t \sigma(\tau)d\tau} \leq N(t) \leq De^{\int_0^t \sigma(\tau)d\tau}, \quad t \geq M.$$

The proof can be found in [6]. We see that the function $\sigma(\tau)$ determines upper and lower bounds of $n(0,t)$ and $N(t)$. Radosavljevic provides conditions that guarantee that equation (2.10) has a unique solution $\sigma$.

**Theorem 2.2.5.** *Suppose that $Q$ is differentiable with respect to $t$ , $Q_t'$ is bounded on $\mathbb{R}^+ \times \mathbb{R}^+$ and $\gamma \in L^\infty(0,M)$, where $M \geq A_\mu$. Moreover, suppose that*

$$\int_0^\infty Q(a,M)e^{-\int_{M-a}^M \gamma(\tau)d\tau}da = 1.$$

*Then the integral equation*

$$\int_0^\infty Q(a,t)e^{-\int_{t-a}^t \sigma(\tau)d\tau}da = 1 \quad t \geq M. \tag{2.11}$$

*has a unique solution $\sigma \in L^\infty(0,\infty)$ such that $\sigma = \gamma$ on $[0,M]$.*

## 2.3 Upper and lower bounds through time-independent models

The non-linear equation (2.11) is usually hard to solve and it is often better to find upper and lower bounds of $e^{\int_0^t \sigma(\tau)d\tau}$ in order to get upper and lower bounds of $n(0,t)$ and $N(t)$. Radosavljevic [6] provides upper and lower bounds on $e^{\int_0^t \sigma(\tau)d\tau}$ by assuming worst and best case scenario on the dead including birth rate $Q(a,t)$. We thus trade exactness of our bounds for simplicity.

**Definition 2.3.1.**

$$Q_+(a) = \sup_{t\geq M} Q(a,t) \quad \text{and} \quad Q_-(a) = \inf_{t\geq M} Q(a,t), \quad a \geq 0. \tag{2.12}$$

The equations

$$\int_0^\infty Q_+(a)e^{-ka}da = 1 \quad \text{and} \quad \int_0^\infty Q_-(a)e^{-ka}da = 1 \tag{2.13}$$

both have unique solutions $k_+$ and $k_-$, respectively since

$$\int_0^\infty Q_+(a)e^{-ka}da \quad \text{and} \quad \int_0^\infty Q_-(a)e^{-ka}da \tag{2.14}$$

are strictly monotonically decreasing function of the parameter $k \in \mathbb{R}$ and tend to 0 and $\infty$ as $k \to \infty$ and $k \to -\infty$, respectively

**Theorem 2.3.1.** *If $k_+$ and $k_-$ are defined by (2.13), then there exist two positive constants $C$ and $D$ such that*

$$Ce^{k_-t} \leq n(0,t) \leq De^{k_+t}, \quad t \geq M.$$

*Proof.* Since

$$\int_0^\infty Q(a,t)e^{-k_-a}da \geq 1 \quad \text{and} \quad \int_0^\infty Q(a,t)e^{-k_+a}da \leq 1, \quad t \geq M,$$

the claim follows from Theorem 2.2.3. □

**Corollary 2.3.1.** *If $k_+$ and $k_-$ are defined by (2.13), then there exist two positive constants $C$ and $D$ such that*

$$Ce^{k_-t} \leq N(t) \leq De^{k_+t}, \; t \geq M.$$

## 2.4 Periodical changes of the environment

Many types of environmental changes in a habitat occurs periodically. We are interested in how these environmental changes impact a given population. For simplicity we consider the case where the death rate is time independent and the birth rate is a periodic function with respect to time. We also assume that the periodic part of the birth rate impacts all individuals the same way regardless of age. With these assumptions we can write $m(a,t)$ and $\mu(a,t)$ as

$$m(a,t) = m(a)(1 + \varepsilon g(t))$$

and

$$\mu(a,t) = \mu(a)$$

where $g(t)$ is periodic with an average value of zero and an amplitude equal to one. The parameter $\varepsilon$ describes the amplitude of the periodic part of the birth rate. We will now find explicit forms of the upper and lower bounds for the number of newborns and for the total population.

**Theorem 2.4.1.** *Suppose that*

$$\begin{aligned} n(0,t) = &\int_0^t m(a,t)e^{-\int_0^a \mu(v,v+t-a)dv} n(0,t-a)da \\ &+ \int_t^\infty m(a,t)e^{-\int_{a-t}^a \mu(v,v+t-a)dv} f(a-t)da, \quad t \geq 0. \end{aligned} \tag{2.15}$$

*where the death rate $\mu(a) = \mu(a,t)$ is independent of time and the birth rate satisfies*

$$m(a,t) = m(a)(1 + \varepsilon g(t)), \quad a, t \geq 0 \tag{2.16}$$

*where $g(t)$ is a periodic function with frequency $A$, average value 0 and amplitude equal to one. The function $g(t)$ can furthermore be expressed with a finite fourier series*

$$g(t) = \sum_{n=-m}^{m} c_n e^{inAt} \tag{2.17}$$

*for some $m \in N$ and coefficients $\{c_n\}_{n=-m}^{m}$ , $c_0 = 0$. Let $k_0$ be the solution to equation*

$$\int_0^\infty Q(a)e^{-k_0 a}da = 1, \tag{2.18}$$

*where*

$$Q(a) = m(a)e^{-\int_0^a \mu(v)dv}, \quad a \geq 0 \tag{2.19}$$

*and let* $k_2$ *be defined as*

$$k_2 = \frac{\int_0^\infty Q(a)e^{-k_0 a} \sum\limits_{n=1}^{m} b_n(a)b_{-n}(a)da - 2\sum\limits_{n=1}^{m} c_n c_{-n}}{\int_0^\infty Q(a)e^{-k_0 a} a da} \tag{2.20}$$

*where*

$$b_n(a) = \frac{c_n(1-e^{-inAa})}{inA\int_0^\infty \phi(a)e^{-inAa}da}$$

*and*

$$\phi(a) = \int_a^\infty Q(a)e^{-k_0 a}da.$$

*Then for sufficiently small* $\varepsilon$ *there exist positive constants* $C, C_1$*, and* $C_2$ *such that*

$$C_1 e^{(k_0+k_2\varepsilon^2 - C\varepsilon^3)t} \leq n(0,t) \leq C_2 e^{(k_0+k_2\varepsilon^2+C\varepsilon^3)t}. \tag{2.21}$$

**Corollary 2.4.1.** *Under assumptions of Theorem 2.4.1 there exist constants* $C$*,* $D_1$ *and* $D_2$ *such that the total population* $N(t)$ *has the following bounds:*

$$D_1 e^{(k_0+\varepsilon^2 k_2 - C\varepsilon^3)t} \leq N(t) \leq d_2 e^{(k_0+\varepsilon^2+C\varepsilon^3)t}$$

*for sufficiently large* $t$*.*

We can express the complex exponentials in terms of cosine and sines to state Theorem 2.4.1 in real form. In that case $g(t)$ will be written as

$$g(t) = \sum_{n=-m}^{m} d_n \cos nAt + e_n \sin nAt$$

where $d_n = 2\,\mathrm{Re}(c_n)$, $e_n = -2\,\mathrm{Im}(c_n)$. Furthermore $b_n = b^*_{-n}$, and $c_n = c^*_{-n}$. Thus we have that

$$k_2 = \frac{\int_0^\infty Q(a)e^{-k_0 a} \sum\limits_{n=1}^{m} |b_n(a)|^2 da - 2\sum\limits_{n=1}^{m} |c_n|^2}{\int_0^\infty Q(a)e^{-k_0 a} a da}, \tag{2.22}$$

where

$$|c_n|^2 = \frac{d_n^2 + e_n^2}{4} \tag{2.23}$$

and

$$|b_n(a)|^2 = \frac{2|c_n|^2(1-\cos nAa)}{n^2A^2((\int_0^\infty \phi(a)\sin nAa da)^2 + (\int_0^\infty \phi(a)\cos nAa da)^2)} \tag{2.24}$$

Inserting equations (2.23) (2.24) in equation (2.22) we get

$$k_2 = \frac{-1}{2\int_0^\infty Q(a)e^{-k_0 a} a da} \sum_{n=1}^{m} \left(d_n^2 + e_n^2\right) \left(1 + \frac{\int_0^\infty Q(a)e^{-k_0 a} \cos nAada - 1}{n^2 A^2 \left(I_c^2(nA) + I_s^2(nA)\right)}\right),$$

where

$$I_c(A) = \int_0^\infty \phi(a) cos(Aa) da$$

and

$$I_s(A) = \int_0^\infty \phi(a) sin(Aa) da.$$

**Example 2.4.1.** If we let $g(t) = cos(At - \gamma)$ then Theorem 2.4.1 holds with

$$k_2 = \frac{-1}{2\int_0^\infty Q(a)e^{-k_0 a} a da} \left(1 + \frac{\int_0^\infty Q(a)e^{-k_0 a} \cos Aada - 1}{A^2 \left(I_1^2(A) + I_2^2(A)\right)}\right)$$

where

$$I_1(A) = \int_0^\infty \phi(a) \cos Aada$$

and

$$I_2(A) = \int_0^\infty \phi(a) \sin Aada$$

which is exactly the same $k_2$ that was calculated by Radosavljevic [6].

*Proof of Theorem 2.4.1.* According to Theorems 2.2.1 and 2.2.2 we can prove the theorem by proving that the following inequalities hold for sufficiently large $t$.

$$\int_0^\infty Q(a)e^{-\int_{t-a}^t \sigma^+(\tau)d\tau}da - \frac{1}{1+\varepsilon g(t)} \leq 0$$

and (2.25)

$$\int_0^\infty Q(a)e^{-\int_{t-a}^t \sigma^-(\tau)d\tau}da - \frac{1}{1+\varepsilon g(t)} \geq 0$$

where the functions $\sigma^\pm$ are defined as

$$\sigma^\pm(t) = k_0 + \varepsilon\sigma_1(t) + \varepsilon^2(k_2 + \sigma_2(t)) \pm C\varepsilon^3 \tag{2.26}$$

where

$$\sigma_1(t) = \sum_{n=-m}^{m} p_n e^{inAt} \tag{2.27}$$

and

$$p_n = \frac{c_n}{-\int_0^\infty \phi(a)e^{-inAa}da} \tag{2.28}$$

and

$$\sigma_2(t) = \sum_{n=-m}^{m}\sum_{k=-m}^{m} \lambda_{n,k}e^{i(n+m)At} \tag{2.29}$$

where

$$\lambda_{n,k} = \begin{cases} \dfrac{\int_0^\infty \phi'(a)b_n(a)b_k(a)da}{2(\int_0^\infty \phi'(a)(1-e^{-i(n_1+n_2)Aa})da)}, & n+k \neq 0 \\ 0, & n+k=0 \end{cases}.$$

We will now express the left hand sides of equation (2.4) using Maclaurin series with respect to $\varepsilon$. If we can prove that the first non zero term of least order is negative respectively positive for large enough $C$ then, since the first term of a Maclaurin series converges much slower then the rest of the sum, we will know that equation (2.4) holds for small enough $\varepsilon$. Expressing the left hand side of equation (2.4) as a Maclaurin series we get after extensive calculations:

$$\int_0^\infty Q(a)e^{-\int_{t-a}^t \sigma^+(\tau)d\tau}da - \frac{1}{1+\varepsilon g(t)} =$$

$$= \int_0^\infty Q(a)e^{-ak_0}da - 1 \tag{2.30}$$

$$- \varepsilon \left( \int_0^\infty Q(a)e^{-ak_0} \int_{t-a}^t \sigma_1(\tau)d\tau da - g(t) \right) \tag{2.31}$$

$$\begin{aligned} &+ \varepsilon^2 \left( \int_0^\infty Q(a)e^{-ak_0} \left( k_2 a + \int_{t-a}^t \sigma_2(\tau)d\tau \right.\right. \\ &\left.\left. + \frac{1}{2}\left( \int_{t-a}^t \sigma_1(\tau)d\tau \right)^2 \right) da - g(t)^2 \right) \end{aligned} \tag{2.32}$$

$$\begin{aligned} &+ \varepsilon^3 \left( \int_0^\infty Q(a)e^{-ak_0} \left( Ca + \frac{1}{6}\int_{t-a}^t \sigma_1(\tau)d\tau \right.\right. \\ &\left.\left. - \left( \int_{t-a}^t k_2 + \sigma_2(\tau)d\tau \right)\left( \int_{t-a}^t \sigma_1(\tau)d\tau \right) \right) da - g(t)^3 d\tau \right) \end{aligned} \tag{2.33}$$

$$+ O(\varepsilon^4).$$

By the definition of $k_0$ (2.18), the first term (2.30) is zero. We will next prove that the second term (2.31) is zero. To do so we study the equation

$$\int_0^\infty Q(a)e^{-ak_0} \int_{t-a}^t \sigma_1(\tau)d\tau da = g(t), \quad t > 0.$$

Using (2.17) and (2.27) this is equivalent to

$$\sum_{n=-m}^{m} \left( \int_0^\infty Q(a)e^{-ak_0}p_n(a) \int_{t-a}^t e^{inA\tau}d\tau da - c_n e^{inAt} \right)$$

$$= \sum_{n=-m}^{m} \left( \int_0^\infty Q(a)e^{-ak_0} \frac{c_n e^{inAt}(1-e^{-inAa})}{inA\int_0^\infty \phi(a)e^{-inAa}da} da \right. \tag{2.34}$$

$$- c_n e^{inAt} \Bigg) = 0$$

In order to calculate the sum (2.34) we simplify each term:

$$\int_0^\infty Q(a)e^{-ak_0} \frac{c_n(1-e^{-inAa})}{inA\int_0^\infty \phi(a)e^{-inAa}da} e^{inAt}da - c_n e^{inAt}$$

$$= e^{inAt}\left(\frac{1}{inA\int_0^\infty \phi(a)e^{-inAa}da}\int_0^\infty Q(a)e^{-ak_0}c_n(1-e^{-inAa})da - c_n\right)$$

$$= e^{inAt}\left(\frac{-1}{inA\int_0^\infty \phi(a)e^{-inAa}da}\int_0^\infty \phi'(a)c_n(1-e^{-inAa})da - c_n\right). \qquad (2.35)$$

Noting that

$$\int_0^\infty \phi'(a)c_n(1-e^{-inAa})da =$$
$$= \left\{\phi(a)c_n(1-e^{-inAa})\right\}_0^\infty - c_n inA\int_0^\infty \phi(a)e^{-inAa}da =$$
$$= -c_n inA\int_0^\infty \phi(a)e^{-inAa}da$$

we have that (2.35) is equal to 0. Thus we have that the third term (2.31) is zero. Next we prove that the fourth term (2.32) is zero for some $\{\lambda_{n,k}\}$. We have the equation

$$\int_0^\infty Q(a)e^{-ak_0}\left(k_2 a + \int_{t-a}^t \sigma_2(\tau)d\tau + \frac{1}{2}\left(\int_{t-a}^t \sigma_1(\tau)d\tau\right)^2\right)da = g(t)^2, \qquad (2.36)$$

which is equivalent to

$$\int_0^\infty Q(a)e^{-ak_0}\left(k_2 a + \int_{t-a}^t \sigma_2(\tau)d\tau\right)da$$
$$= g(t)^2 - \frac{1}{2}\int_0^\infty Q(a)e^{-ak_0}\left(\int_{t-a}^t \sigma_1(\tau)d\tau\right)^2 da.$$

We separate $g(t)^2$ and $(\int_{t-a}^t \sigma_1(\tau)d\tau)^2$ into a constant average term and a periodic term with zero average:

$$g(t)^2 = \sum_{n_1=-m}^{m}\sum_{n_2=-m}^{m} c_{n_1}c_{n_2}e^{i(n_1+n_2)At}$$

$$= 2\sum_{n=1}^{m} c_n c_{-n} + \sum_{n_1=-m}^{m} \sum_{\{n_2\in[-m,m]:n_1+n_2\neq 0\}} c_{n_1} c_{n_2} e^{i(n_1+n_2)At}$$

and

$$\begin{aligned}\left(\int_{t-a}^{t} \sigma_1(\tau)d\tau\right)^2 &= \left(\int_{t-a}^{t} \sum_{n=-m}^{m} p_n e^{inA\tau} d\tau\right)^2 = \left(\sum_{n=-m}^{m} p_n e^{int} \frac{(1-e^{-inAa})}{inA}\right)^2 \\ &= 2\sum_{n=1}^{m} p_n p_{-n} \frac{|1-e^{inAa}|^2}{n^2} \\ &\quad + \sum_{\{(n_1,n_2):n_1+n_2\neq 0\}} p_{n_1} p_{n_2} e^{i(n_1+n_2)At} \frac{(1-e^{-in_1Aa})(1-e^{-in_2Aa})}{n_1 n_2} \\ &= 2\sum_{n=1}^{m} b_n(a) b_{-n}(a) + \sum_{\{(n_2,n_1):n_1+n_2\neq 0\}} b_{n_1}(a) b_{n_2}(a) e^{i(n_1+n_2)At}.\end{aligned}$$

We now have that (2.36) is equivalent to

$$\begin{aligned}&k_2 \int_0^\infty \phi'(a) a da + \int_0^\infty \phi'(a) \int_{t-a}^{t} \sigma_2(\tau) d\tau da \\ &= 2\sum_{-m}^{m} c_n c_{-n} - \int_0^\infty Q(a) e^{-ak_0} \sum_{n=1}^{m} b_n(a) b_{-n}(a) da \\ &\quad - \frac{1}{2}\int_0^\infty Q(a) e^{-ak_0} \sum_{\{(n_1,n_2):n_1+n_2\neq 0\}} b_{n_1}(a) b_{n_2}(a) e^{i(n_1+n_2)At} da.\end{aligned}$$

From the definition of $k_2$ (2.20), we have that this is equivalent to

$$\int_0^\infty \phi'(a) \int_{t-a}^{t} \sigma_2(\tau) d\tau da = \frac{1}{2}\int_0^\infty \phi'(a) \sum_{\{(n_1,n_2):n_1+n_2\neq 0\}} b_{n_1} b_{n_2} e^{i(n_1+n_2)At} da.$$

Using our definition of $\sigma_2$ we get

$$\begin{aligned}&\int_0^\infty \phi'(a) \int\limits_{t-a}^{t} \sum_{n_1=-m}^{m} \sum_{n_2=-m}^{m} \lambda_{n_1,n_2} e^{i(n_1+n_2)A\tau} d\tau da \\ &= \frac{1}{2}\int_0^\infty \phi'(a) \sum_{\{(n_1,n_2):n_1+n_2\neq 0\}} b_{n_1} b_{n_2} e^{i(n_1+n_2)At} da,\end{aligned}$$

which is equivalent to

$$\begin{aligned}
&\int_0^\infty \phi'(a) \sum_{n_1=-m}^{m} \sum_{n_2=-m}^{m} \lambda_{n_1,n_2}(1-e^{-i(n_1+n_2)Aa})e^{i(n_1+n_2)At}da \\
&\quad = \frac{1}{2}\int_0^\infty \phi'(a) \sum_{\{(n_1,n_2):n_1+n_2\neq 0\}} b_{n_1}b_{n_2}e^{i(n_1+n_2)At}da
\end{aligned}$$

and by the definition of $\lambda_{n_1,n_2}$ we can finally conclude that (2.32) is zero. Next we study the fifth term (2.33)

$$\begin{aligned}
&\int_0^\infty Q(a)e^{-ak_0}\left(Ca + \frac{1}{6}\int_{t-a}^{t}\sigma_1(\tau)d\tau - \int_{t-a}^{t} k_2+\sigma_2(\tau)d\tau \int_{t-a}^{t}\sigma_1(\tau)d\tau\right)da \\
&\qquad - g(t)^3 \\
&\quad = (C - k_2\int_{t-a}^{t}\sigma_1(\tau)d\tau)\int_0^\infty Q(a)e^{-ak_0}ada \\
&\qquad - \int_0^\infty Q(a)e^{-ak_0}\left(\frac{1}{6}\int_{t-a}^{t}\sigma_1(\tau)d\tau + \int_{t-a}^{t}\sigma_2(\tau)d\tau\int_{t-a}^{t}\sigma_1(\tau)d\tau\right)da \\
&\qquad - g(t)^3.
\end{aligned}$$

Since $Q(a)$ has compact support we can conclude that

$$\int_0^\infty Q(a)e^{-ak_0}ada$$

and

$$\int_0^\infty Q(a)e^{-ak_0}\left(\frac{1}{6}\int_{t-a}^{t}\sigma_1(\tau)d\tau + \int_{t-a}^{t}\sigma_2(\tau)d\tau\int_{t-a}^{t}\sigma_1(\tau)d\tau\right)da,$$

as functions of $t$, are bounded. Furthermore we know that $g(t)$ is bounded. Thus for sufficiently large positive $C$, we have that (2.33) is positive and for sufficiently large negative $C$ we have that (2.33) is negative. Thus we can now conclude that for some constant $D_1, D_2$, and $D$ we have that

$$D_1e^{(k_0+k_2\varepsilon^2-D\varepsilon^3)t+h(t)} \leq n(0,t) \leq D_2e^{(k_0+k_2\varepsilon^2+D\varepsilon^3)t+h(t)}$$

for some bounded function $h(t)$ if $\varepsilon > 0$ is sufficiently small. This finally implies that for some positive constants $C_1, C_2$, and $C$ we have that

$$C_1e^{(k_0+k_2\varepsilon^2-C\varepsilon^3)t} \leq n(0,t) \leq C_2e^{(k_0+k_2\varepsilon^2+C\varepsilon^3)t}$$

if $\varepsilon > 0$ is small enough. □

It is interesting to note that the individual impact of each term in $g(t)$ on $k_2$ is added on to each other to get the total impact of $g(t)$ on $k_2$. If we want to study the behavior of $k_2$ we just have to study

$$k_2^*(A) = \frac{-1}{2\int_0^\infty Q(a)e^{-k_0 a}da}\left(1 + \frac{\int_0^\infty Q(a)e^{-k_0 a}\cos Aada - 1}{A^2\left(I_1^2(A) + I_2^2(A)\right)}\right).$$

We are especially interested in how the sign of the number $k_2^*(A)$ varies with the frequencies $A$ since this impacts if the population will go extinct or not. In order to understand the behavior of $k_2^*(A)$ we need to understand how functions of the type

$$h(A) = \int_0^\infty f(x)e^{iAx}dx = \int_0^\infty f(x)\cos Axdx + i\int_0^\infty f(x)\sin Axdx$$

where $f(x) \in C^1(0,\infty)$ decreases monotonically from one to zero at some interval $[a,b]$, $(a < b)$ and remains constant otherwise.

In fact it turns out from Riemann–Lebesgue lemma that in general $h(A)$ converges to zero. Using Riemann-lebesgues lemma we also see that the rate of convergence is $\frac{1}{A}$. We have that

$$\left|\int_0^\infty f(x)e^{iAx}\,dx\right| \leq \frac{1}{|A|}\int_0^\infty |f'(x)|dx \leq \frac{1}{A} \to 0, \quad \text{as } A \to \pm\infty.$$

Thus by using partial integration and the inverse triangle inequality we get that their for each $A$ exists a constant $C(A) > 0$ such that

$$\begin{aligned}\left|\int_0^\infty f(x)e^{iAx}dx\right| &= \left|\left[-f(x)\frac{1}{A}e^{iAx}\right]_0^\infty + \int_0^\infty f'(x)\frac{1}{A}e^{iAx}dx\right| \\ &= \left|\frac{1}{A} + \frac{1}{A}\int_0^\infty f'(x)e^{iAx}dx\right| \\ &\geq \frac{\left|1 - \left|\int_0^\infty f'(x)e^{iAx}dx\right|\right|}{A} \\ &\geq \frac{C(A)}{A} \end{aligned} \tag{2.37}$$

So we can conclude that there for each $A$ exists a constant, $C(A) > 0$ such that

$$\frac{C(A)}{A} \leq \left|\int_0^\infty f(x)e^{iAx}dx\right| \leq \frac{1}{A}, \quad A > 0 \tag{2.38}$$

and since $\left|\int_0^\infty f'(x)e^{iAx}dx\right| \to 0$ as $A \to$ we can also see that if $A \to \infty$ then $\sup\{C(A) : \text{the inequality (2.38) is satisfied}\}$ converge to one. We can thus conclude that

$$A \left| \int_0^\infty f(x) e^{iAx} dx \right| \to 1 \text{ as } A \to \infty.$$

We can now conclude that $k_2^*(A) \to 0$ as $A \to \infty$.

According to Theorem 2.4.1, since $\varepsilon$ is small, the long term stability of the population is primarily determined by $k_0$. In the case where $k_0$ is close enough to or equal to one the long term behavior is determined by the sign of $k_2$. If $k_2$ is negative then the population tends to zero and if $k_2$ is positive the population growths indefinitely.

In the appendix we can find a table of real life data of vital rates of four different kinds of populations. The table shows the mean birth rate $m$ and the survival propability $s$. The survival rate is defined by

$$s(a) = e^{-\int_{a-1}^{a} \mu(v) dv}, \quad a \in [1, A_\mu].$$

Figure 4.1 and figure 4.2 shows graphs of $k_2^*(A)$ for the different life histories. From the graphs we can see that the the sign of $k_2$ varies with $A$. This implies that periodic effects on birth rate can have both positive and negative effects on population growth.

## 2.5 Generalisation to infinite Fourier series

In order to generalise Theorem 2.4.1 to include the case where $g(t)$ can be expressed as an infinite series

$$g(t) = \sum_{n=-\infty}^{\infty} c_n e^{inAt}$$

we have to assure ourselves that all the sums in the proof of Theorem 2.4.1 converges as the upper and lower bounds of the summations goes to infinity. The most demanding of these sums is

$$\sigma_1(t) = \sum_{n=-\infty}^{\infty} \frac{c_n e^{inAt}}{-\int_0^\infty \phi(a) e^{-inAa} da}$$

For this sum we have to note that according to Lebesgue's lemma since $\phi(a) \in L^1$ we have that

$$\int_0^\infty \phi(a) e^{-inAa} da$$

tends to zero as $n \to \pm\infty$ more precisely we have from (2.38) that there for each $A$ exist a constant $C(A) > 0$ such that,

$$\frac{C(A)}{nA} \leq \int_0^\infty \phi(a) e^{-inAa} da \leq \frac{1}{nA} \quad , \; n \in \mathbb{Z}$$

This tells us that if $\{c_n\}_{n=-\infty}^{\infty}$ converges faster then the rate of $\frac{1}{n^2}$ we know that $\sigma_1(t)$ converges. This implies that the theorem holds if $g$ is in the 2-Hölder class. If $\{c_n\}_{n=-\infty}^{\infty}$ converges slower then $\frac{1}{n^2}$ then $\sigma_1(t)$ may or may not converge. If $\sigma_1(t)$ converges then all other sums in the proof of Theorem (2.4.1) converges and thus we know that the Theorem (2.4.1) holds. If $\sigma_1(t)$ does not converge we do not yet know if the bound still applies or not. This requires further investigation.

# Chapter 3

# Logistic population model

## 3.1 Modelling density dependence

One important fact that is ignored in von Foerster's model is that the environment of the population is not able to sustain a population that is to big. We can also model this by introducing the assumption that the death rate is dependent on the population size. So we get a balance equation looking like this:

$$\frac{\partial n(a,t)}{\partial a} + \frac{\partial n(a,t)}{\partial t} = \mu(a,t,n(t))n(a,t). \tag{3.1}$$

Equation (3.1) gives us a general model. An interesting question is how the death rate is dependent on the population size. Obviously we want our model to satisfy that the death rate increases with increasing population size. Our intuition should also let us believe that the impact of an increased population size should be bigger if the population size already are in the range of overpopulation. We also believe that even though the population size is small compared to the environment, there is still going to exist a death rate. The next balance equation we will study, satisfying all the above, taken from [5], is:

$$\frac{\partial n(a,t)}{\partial a} + \frac{\partial n(a,t)}{\partial t} = -\mu(a)n(a,t)\left(1 + \frac{n(a,t)}{L(a,t)}\right) \quad a,t > 0 \tag{3.2}$$

The boundary conditions and initial condition are

$$n(0,t) = \int_0^\infty m(a,t)n(a,t)da, \quad t > 0, \tag{3.3}$$

and

$$n(a,0) = f(a), \quad a > 0, \tag{3.4}$$

It is important to note that the balance equation (3.2) assumes that the competition only occurs between individuals with the same age and effects only the death rate. This is generally not the case but the assumption is still justified because it simplifies the analysis and still give results close to real life scenarios. The equation is non-linear but fortunately we can still use the method of integrating factor to get a renewal equation similar to the one in our first model. For simplicity we will use the notations

$$\pi(a,t) = \int_0^a \frac{\mu(v,v+t-a)e^{-\int_0^v \mu(s,s+t-a)ds}}{L(v,v+t-a)}, \quad t>a, \tag{3.5}$$

$$\phi(a,t) = e^{\int_0^{a-t}\mu(v,v+t-a)dv} \int_{a-t}^a \frac{\mu(v,v+t-a)e^{-\int_0^v \mu(s,s+t-v)ds}}{L(v,v+t-a)} dv, \quad a>t, \tag{3.6}$$

$$\psi(a,t) = m(a,t)e^{-\int_{a-t}^a \mu(s,s+t-a)dv}, \quad a>t. \tag{3.7}$$

**Theorem 3.1.1.** *Let $n(a,t)$ be a solution to the (3.2) with boundary and initial conditions (3.3) and (3.4). Then*

$$n(0,t) = Kn(0,t) + Ff(t), \quad t \geq 0, \tag{3.8}$$

*where*

$$Kn(0,t) = \int_0^t \frac{Q(a,t)n(0,t-a)}{1+n(0,t-a)\pi(a,t)} da,$$

*and*

$$Ff(t) = \int_t^\infty \frac{\psi(a,t)f(a-t)}{1+f(a-t)\phi(a,t)} da.$$

*For other values of a, n(a,t) can be found by*

$$n(a,t) = \begin{cases} \frac{n(0,t-a)e^{-\int_0^a \mu(v,v+t-a)dv}}{1+n(0,t-a)\pi(a,t)}, & a<t \\ \frac{f(a-t)e^{-\int_0^a \mu(v,v+t-a)dv}}{1+f(a-t))\psi(a,t)}, & a>t. \end{cases}$$

*Proof.* If we parameterize $a$ and $t$ with the variable $x$ in the following way: $a = x$ $t = x + C$ ,where $C$ is a constant, we will get according to the chain rule:

$$\begin{aligned} \frac{dz(x)}{dx} &= /z(x) = n(x,x+C)/ = \frac{\partial n(x,x+C)}{\partial x} = \frac{da}{dx}\frac{\partial n(a,t)}{\partial a} + \frac{dt}{dx}\frac{\partial n(a,t)}{\partial t} \\ &= \frac{\partial n(a,t)}{\partial a} + \frac{\partial n(a,t)}{\partial t} = -\mu(x,x+C)z(x)\left(1+\frac{z(x)}{L(x,x+C)}\right) \end{aligned} \tag{3.9}$$

so

$$\frac{dz(x)}{dx} + \mu(x, x+C)z(x) = \frac{-\mu(x, x+C)z(x)^2}{L(x, x+C)}.$$

By multiplying by $e^{\int \mu(x,x+C)dx}$ on both sides we get:

$$\begin{aligned} &e^{\int \mu(x,x+C)dx}\frac{dz(x)}{dx} + e^{\mu(x,x+C)}\mu(x, x+C)z(x) \\ &= e^{\int \mu(x,x+C)dx}\frac{-\mu(x, x+C)z(x)^2}{L(x, x+C)} \end{aligned}$$

so

$$\left(e^{\int \mu(x,x+C)dx}z(x)\right)' = e^{\int \mu(x,x+C)dx}\frac{-\mu(x, x+C)z(x)^2}{L(x, x+C)}$$

so

$$\frac{\left(e^{\int \mu(x,x+C)dx}z(x)\right)'}{\left(e^{\int \mu(x,x+C)dx}z(x)\right)^2} = -\frac{e^{-\int \mu(x,x+C)dx}\mu(x, x+C)}{L(x, x+C)}$$

so for some constant $K$ we have

$$-\frac{1}{e^{\int \mu(x,x+C)dx}z(x)} + K = -\int \frac{e^{-\int \mu(x,x+C)dx}\mu(x, x+C)}{L(x, x+C)}dx.$$

Since we have the condition that $a, t > 0$, we have to consider two cases when we define $K$ and the boundaries to the integrals. In the case of $C > 0$, that is $a < t$, we have

$$-\frac{1}{e^{\int_0^x \mu(v,v+C)dv}z(x)} + \frac{1}{z(0)} = -\int_0^x \frac{e^{-\int_0^x \mu(v,v+C)}\mu(x, x+C)}{L(x, x+C)}dx.$$

Rearranging the terms we get

$$z(x) = \frac{z(0)e^{-\int_0^x \mu(v,v+C)dv}}{1 + z(0)\int_0^x \frac{e^{-\int_0^s \mu(v,v+C)dv}\mu(s,s+C)}{L(s,s+C)}ds}.$$

Returning to old variables gives us

$$n(a,t) = \frac{n(0, t-a)e^{-\int_0^a \mu(v,v+t-a)dv}}{1 + n(0, t-a)\int_0^a \frac{e^{-\int_0^s \mu(v,v+t-a)dv}\mu(s,s+t-a)}{L(s,s+t-a)}ds}, \quad a < t.$$

In the case $C \leq 0$ or in original variables $a \geq t$, we have that

$$-\frac{1}{e^{\int_0^x \mu(v,v+C)dv} z(x)} + \frac{1}{z(-C)} = -\int_{-C}^{x} \frac{e^{-\int_{-C}^{v} \mu(s,s+C)ds} \mu(v,v+C)}{L(v,v+C)} dx$$

which gives us

$$z(x) = \frac{z(-C)e^{-\int_{-C}^{x} \mu(v,v+C)dv}}{1 + z(-C)\int_{-C}^{x} \frac{e^{-\int_{-C}^{s} \mu(v,v+C)dv} \mu(s,s+C)}{L(s,s+C)} ds}.$$

In terms of $a$ and $t$ this becomes

$$n(a,t) = \frac{f(a-t)e^{-\int_{a-t}^{a} \mu(v,v+t-a)dv}}{1 + f(a-t)\int_{a-t}^{a} \frac{e^{-\int_{a-t}^{s} \mu(v,v+t-a)dv}}{L(s,s+t-a)} ds}, \quad t > a.$$

Using the boundary condition (3.3) and our notations (3.5),(3.6),(3.7) we get

$$n(a,t) = \begin{cases} \frac{n(0,t-a)e^{-\int_0^a \mu(v,v+t-a)dv}}{1+n(0,t-a)\pi(a,t)}, & a < t \\ \frac{f(a-t)e^{-\int_{a-t}^{a} \mu(v,v+t-a)dv}}{1+f(a-t)\phi(a,t)} & a \geq t \end{cases}$$

and

$$\begin{aligned} n(0,t) = & \int_0^t \frac{m(a,t)n(0,t-a)e^{-\int_0^a \mu(v,v+t-a)dv}}{1+n(0,t-a)\pi(a,t)} da \\ & + \int_t^{\infty} \frac{m(a,t)f(a-t)e^{-\int_{a-t}^{a} \mu(v,v+t-a)dv)}}{1+f(a-t)\phi(a,t)} da. \end{aligned}$$

□

The renewal equation (3.8) is the equivalent to the renewal equation (2.5) in the first model and can be interpreted in the same way. In [5] Radosavljevic provides proof for existence and uniqueness of (3.8). Radosavljevic proves existence by using the fact that the iterative sequence defined by

$$n_{k+1} = Kn_k + Ff, \quad n_0 = n^-,$$

where $n^-$ is a lower solution, is increasing yet bounded and thus converges towards what must be a solution.

Our second population model differs from our first by having the property that the solution $n(a,t)$ is bounded.

**Theorem 3.1.2.** *Let $n$ be a solution to Equation (3.8) and let the functions $n^*$, $n_* \in L^\infty(0,\infty)$ satisfy $0 < c_1 \leq n_*$, $n^* \leq c_2 < \infty$.*

*(a) If $Kn^*(0,t) \leq n^*(0,t)$ for $t > M^* > 0$, then there exists positive constants $C_1$ and $\alpha_1$ such that*

$$n(0,t) \leq n^*(0,t)(1 + C_1 e^{-\alpha_1 t}), \quad t \geq 0.$$

*(b) If $Kn_*(0,t) \geq n_*(0,t)$ for $t > M^* > 0$, then there exists positive constants $C_2$ and $\alpha_2$ such that*

$$n(0,t) \geq n_*(0,t)(1 - C_2 e^{-\alpha_2 t}), \quad t \geq 0.$$

A proof of Theorem 3.1.2 can be found in [5]. Theorem 3.1.2 tells us that $n^*$ and $n_*$ describes upper and lower bounds of $n(0,t)$. The net reproductive rate $R_0$ is defined by

$$R_0 = \int_0^\infty Q(a)da$$

In the following theorems we will use the root $n^*$ of the equation

$$\int_0^\infty \frac{Q(a)}{1 + n^*\pi(a)} da = 1 \tag{3.10}$$

One can rather easily conclude the following lemma.

**Lemma 3.1.3.** *Let $Q$ be a continuous function. If $R_0 > 1$, the integral equation (3.10) has a unique solution $n^* > 0$. If $R_0 \leq 1$, equation (3.10) has no positive solution.*

## 3.2 Asymptotics of newborns and of the total population in the case of periodic vital rates

In this section, we will use Theorem 3.1.2 to study the asymptotic behavior of the number of newborns living in an periodical changing environment. For simplicity we constrain ourself to the case where we assume that the birth rate is periodic in time and that the death rate is time independent. To simplify even more we assume that the regulating function $L$ is constant. We get the following constraints:

$$m(a,t) = m_0(a) + \varepsilon \sum_{n=-N}^{N} a_n e^{-inAt} m_1(a), \quad a, t > 0, \tag{3.11}$$

$$\mu(a,t) = \mu(a), \tag{3.12}$$
$$L(a,t) = L, \qquad L > 0 \tag{3.13}$$

where $\varepsilon > 0$ and $m_0$, $m_1$ satisfy assumption (i). We use the notation

$$Q_i(a) = m_i(a)e^{-\int_0^\infty \mu(v)dv}, \quad i = 1,2$$
$$\pi(a) = \frac{1}{L}\left(1 - e^{-\int_0^\infty \mu(v)dv}\right).$$

**Theorem 3.2.1.** *Let $n$ be a solution to equation 3.8 where the vital rates and the regulating function are given by (3.11) (3.12) and (3.13). If $\int_0^\infty Q_0(a)da > 1$ then*

$$n(t) = n_0^* + \varepsilon\left(\sum_{-N}^{N} a_n b_n e^{inAt}\right) + \varepsilon^2\left(k_2 + \sum_{\{(n_1,n_2):n_1+n_2\neq 0\}} c_{n_1,n_2} e^{i(n_1+n_2)At}\right) + O(\varepsilon^3)$$

*where $n_0^*$ is the positive solution to the equation*

$$\int_0^\infty \frac{Q_0(a)}{1 + n_0^*\pi(a)da} = 1 \tag{3.14}$$

*and the parameters $b_n$, $c_{n_1,n_2}$, $k_2$ are given by*

$$b(A) = \frac{\int_{a_m}^{A_m} \frac{n_0^* Q_1(a)}{1+n_0^*\pi(a)} da}{1 - \int_{a_m}^{A_m} \frac{Q_0(a)e^{-iAa}}{(1+n_0^*\pi(a))^2} da},$$

$$c_{n_1,n_2} = \frac{a_{n_1}a_{n_2}\left(\int\limits_{a_m}^{A_m} \frac{Q_0(a)b(An_1)b(An_2)e^{-i(n_1+n_2)Aa}\pi(a)}{(1+n_0^*\pi(a))^3} - \frac{b(An_2)e^{-in_2Aa}Q_1(a)}{(1+n_0^*\pi(a))^2} da\right)}{\int\limits_{a_m}^{A_m} \frac{Q_0(a)e^{-i(n_1+n_2)Aa}}{(1+n_0^*\pi(a))^2} da - 1}, \tag{3.15}$$

*and*

$$k_2 = \frac{2\sum\limits_{n=1}^{N} a_n a_{-n}\left(\int\limits_{a_m}^{A_m} \frac{Q_1(a)Re(b(nA)e^{-nAa})}{(1+n_0^*\pi(a))^2} - \frac{|b(nA)|^2 Q_0(a)\pi(a)}{(1+n_0^*\pi(a))^3} da\right)}{1 - \int\limits_{a_m}^{A_m} \frac{Q_0(a)}{(1+n_0^*\pi(a))^2} da} \tag{3.16}$$

Theorem 3.2.1 tells us that $n(0,t)$, for large $t$, has a periodic behavior with an average of $n_0^* + \varepsilon^2 k_2$. The number $n_0^*$ is not dependent on the periodic term while $k_2$ is. If $k_2$ is positive, according to Theorem 3.2.1, the periodic term has a positive effect on the population. In the other case if $k_2$ is negative then the population is effected negatively. We can only guaranty that the theorem holds if $\varepsilon$ is small enough. This indicates that the effect on the population is small.

The complex form of theorem 3.2.1 provides a compact way of writing. However the complex form can be rather hard to interpret so we next express it in a real form. When expressing theorem 3.2.1 in the real case we use the following notations:

$$I = \int_{a_m}^{A_m} \frac{n_0^* Q_1(a)}{1 + n_0^* \pi(a)} da,$$

$$I_c(A) = \int_{a_m}^{A_m} \frac{Q_0(a) \cos Aa}{(1 + n_0^* \pi(a))^2} da, \qquad I_s(A) = \int_{a_m}^{A_m} \frac{Q_0(a) \sin Aa}{(1 + n_0^* \pi(a))^2} da,$$

$$\begin{aligned}
&\lambda_x^{n_1,n_2}(A) = \\
&\int_{a_m}^{A_m} \frac{Q_0(a)(d(n_1A)d(n_2A) - e(n_1A)e(n_2A))\pi(a)\cos(n_1+n_2)Aa}{2(1+n_0^*\pi(a))^3} da \\
&- \int_{a_m}^{A_m} \frac{Q_0(A)(d(n_1A)e(n_2A) + d(n_2A)e(n_1A))\pi(a)\sin(n_1+n_2)Aa}{2(1+n_0^*\pi(a))^3} da \\
&- \int_{a_m}^{A_m} \frac{(x_{n_1} d(n_2A) - y_{n_1} e(n_2A))Q_1(a)\cos n_2Aa}{2(1+n_0^*\pi(a))^2} da, \\
&- \int_{a_m}^{A_m} \frac{(x_{n_1} e_{n_1} + y_{n_1} d_{n_1})Q_1(a)\sin n_2Aa}{2(1+n_0^*\pi(a))^2} da,
\end{aligned}$$

and

$$\begin{aligned}
&\lambda_y^{n_1,n_2}(A) = \\
&\int_{a_m}^{A_m} \frac{Q_0(a)((d(n_1A)e(n_2A) + e(n_1A)d(n_2A)\cos(n_1+n_2)Aa}{2(1+n_0^*\pi(a))^3} da \\
&+ \int_{a_m}^{A_m} \frac{Q_0(a)(d(n_1A)d(n_2A) - e(n_1A)e(n_2A)))\pi(a)\sin(n_1+n_2)Aa}{2(1+n_0^*\pi(a))^3} da
\end{aligned}$$

$$-\int_{a_m}^{A_m} \frac{(x_{n_1} e(n_2A) + y_{n_1} d(n_2A))Q_1(a)\cos n_2Aa}{2(1+n_0^*\pi(a))^2} da$$
$$-\int_{a_m}^{A_m} \frac{(x_{n_1} e(n_2A) + y_{n_1} d(n_2A)))Q_1(a)\sin n_2Aa}{2(1+n_0^*\pi(a))^2} da.$$

Now we can express Theorem 3.2.1 in real form. Expressing Theorem 3.2.1 in real form. We get the following expressions.

$$g(t) = \sum_{n=1}^{N} x_n \cos nAt + y_n \sin nAt$$

$$\begin{aligned} n(t) &= n_0^* \\ &+ \varepsilon \left( \sum_{1}^{N} (x_n d(nA) + y_n e(nA)) \cos At - (y_n d(nA) - x_n e(nA)) \sin At \right) \\ &+ \varepsilon^2 \left( k_2 + \sum_{\{(n_1,n_2):n_1+n_2 \neq 0\}} f_{n_1,n_2} \cos{(n_1+n_2)At} + g_{n_1,n_2} \sin{(n_1+n_2)At} \right) + O(\varepsilon^3) \end{aligned}$$

where $n_0^*$ is the positive solution to the equation.

$$\int_0^\infty \frac{Q_0(a)}{1+n_0^*\pi(a)} da = 1, \tag{3.17}$$

and

$$d(nA) = \frac{I(1-I_c(nA))}{(1-I_c(nA))^2 + (I_s(nA))^2},$$

$$e(nA) = \frac{II_s(nA)}{(1-I_c(nA))^2 + (I_s(nA))^2},$$

$$f_{n_1,n_2}(A) = \frac{-\lambda_x^{n_1,n_2}(1-I_c^{n_1+n_2}(A)) + \lambda_y^{n_1,n_2} I_s((n_1+n_2)A)}{(1-I_c((n_1+n_2)A))^2 + (I_s((n_1+n_2)A))^2},$$

$$g_{n_1,n_2}(A) = \frac{-\lambda_x^{n_1,n_2}(A) I_s((n_1+n_2)A) - \lambda_y^{n_1,n_2}(A)(1-I_c((n_1+n_2)A))}{(1-I_c((n_1+n_2)A)) + (I_s((n_1+n_2)A))^2},$$

and

$$k_2 = \frac{\sum_{n=1}^{N}\left(x_n^2 + y_n^2\right)\left(\int_{a_m}^{A_m} \frac{Q_0(a)\pi(a)}{(1+n_0^*\pi(a))^3} - \frac{Q_1(a)d(nA)\cos Ana - e(nA)\sin Ana}{(1+n_0^*\pi(a))^2} da\right)}{2\left(\int_{a_m}^{A_m} \frac{Q_0(a)}{(1+n_0^*\pi(a))^2} da - 1\right)}.$$

If we consider the case where $g(t) = \cos At$ then we have

$$\begin{aligned} n(t) &= n_0^* + \varepsilon\left(\sum_1^N d_n \cos At + e_n \sin At\right) \\ &+ \varepsilon^2\left(k_2^* + \sum_{\{(n_1,n_2):n_1+n_2\neq 0\}} f_{n_1,n_2}\cos(n_1+n_2)At + g_{n_1,n_2}\sin(n_1+n_2)At\right) + O(\varepsilon^3) \end{aligned}$$

where

$$d(A) = \frac{I(1-I_c(A))}{(I_c(A))^2 + (I_s(A))^2}, \quad e(A) = \frac{II_s(A)}{(1-I_c(A))^2 + (I_s(A))^2},$$

$$\begin{aligned} f_{1,1}(A) &= \frac{-\lambda_x^{1,1}(A)(1-I_c^2(A)) + \lambda_y^{1,1}(A)I_s^2(A)}{(1-I_c^2(A))^2 + (I_s^2(A))^2}, \\ g_{1,1}(A) &= \frac{-\lambda_x^{1,1}(A)I_s^2(A) - \lambda_y^{1,1}(A)(1-I_c^2(A))}{(I_s^2(A))^2 + (1-I_c^2(A))^2}, \end{aligned}$$

and

$$k_2^*(A) = \frac{\int_{a_m}^{A_m} \frac{\left(d_1^2+e_1^2\right)Q_0(a)\pi(a)}{(1+n_0^*\pi(a))^3} da - \int_{a_m}^{A_m} \frac{Q_1(a)(d_1\cos Ana + e_1 \sin Ana)}{(1+n_0^*\pi(a))^2} da}{2\left(\int_{a_m}^{A_m} \frac{Q_0(a)}{(1+n_0^*\pi(a))^2} da - 1\right)} \tag{3.18}$$

where

$$I_c^1(A) = \int_{a_m}^{A_m} \frac{Q_0(a)\cos Aa}{(1+n_0^*\pi(A))^2} da, \quad I_s^1(A) = \int_{a_m}^{A_m} \frac{Q_0(a)\sin Aa}{(1+n_0^*\pi(A))^2} da,$$

$$\lambda_x^{1,1}(A) = \frac{1}{2}\int_{a_m}^{A_m} \frac{Q_0(a)(d_1^2 - e_1^2)\cos 2Aa - 2d_1e_1\pi(a)\sin 2Aa}{(1+n_0^*\pi(a))^3} da$$

$$-\frac{1}{2}\int_{a_m}^{A_m}\frac{Q_1(a)(d_1\cos Aa-e_1\sin Aa)}{(1+n_0^*\pi(a))^2},$$

and

$$\begin{aligned}\lambda_y^{1,1}(A)=&\frac{1}{2}\int_{a_m}^{A_m}\frac{Q_0(A)\pi(a)((2d_1e_1)\cos 2Aa+(d_1^2-e_1^2)\sin 2Aa)}{(1+n_0^*\pi(a))^3},\\ &-\frac{1}{2}\int_{a_m}^{A_m}\frac{Q_1(a)\,(e_1\cos Aa+e_1\sin Aa)}{(1+n_0^*\pi(a))^2}.\end{aligned}$$

The average numbers of newborns is defined by

$$n_{av}=\frac{A}{2\pi}\int_0^{2\pi/A}n(t)dt.$$

**Corollary 3.2.1.** *Let the assumptions of Theorem 3.2.1 hold. If* $\int_{a_m}^{A_m} Q_0(a)da>1$ *and* $\varepsilon>0$ *is small enough, then the average number of newborn is*

$$n_{av}=n_0^*+\varepsilon^2k_2+O(\varepsilon^3).$$

*Moreover, the average total population is*

$$N_{av}=(n_0^*+\varepsilon^2k_2)\int_0^{A_\mu}\frac{e^{-\int_0^a\mu(v)dv}}{1+n_{av}\pi(a)}da+O(\varepsilon^3).$$

## 3.3 Proof of Theorem 3.2.1

*Proof.* According to Theorem 3.1.2 it is sufficient to check that the functions $n^{\pm}$ given by

$$n^{\pm}(t) = n_0^* + \varepsilon \sum_{n=-N}^{N} b_n e^{int} + \varepsilon^2 \left( k_2 + \sum_{n_1=-N}^{N} \sum_{n_2=-N}^{N} c_{n_1,n_2} e^{int} \right) \pm C\varepsilon^3$$

where $a_0 = b_0 = c_0 = 0$ satisfies the inequalities

$$Kn^+(t) \leq n^+(t), \quad \text{and} \quad Kn^-(t) \geq n^-(t) \tag{3.19}$$

for sufficiently large $t$. We use the notation:

$$f(a,t) = \sum_{n=-N}^{N} a_n e^{int}, \tag{3.20}$$

$$p_1(t) = \sum_{n=-N}^{N} a_n b(nA) e^{int}, \tag{3.21}$$

$$p_2(t) = k_2 + \sum_{n_1=-N}^{N} \sum_{n_2=-N}^{N} c_{n_1,n_2} e^{int}, \tag{3.22}$$

and

$$Q_1(a) = m_1(a) e^{-\int_0^a \mu(v)dv}. \tag{3.23}$$

Now we have that

$$\begin{aligned} &Kn^{\pm}(t) - n^{\pm}(t) = \\ &= \int_{a_m}^{A_m} \frac{(Q_0(a) + \varepsilon f(a,t) Q_1(a))(n_0^* + \varepsilon p_1(t-a) + \varepsilon^2 p_2(t-a) \pm C\varepsilon^3}{1 + (n_0^* + \varepsilon p_1(t-a) + \varepsilon^2 p_2(t-a) \pm C\varepsilon^3)\pi(a)} da \\ &\quad - (n_0^* + \varepsilon p_1(t) + \varepsilon^2 p_2(t) \pm C\varepsilon). \end{aligned}$$

Using Maclaurin series expansion and grouping terms with same powers of $\varepsilon$ we get:

$$Kn^{\pm}(t) - n^{\pm}(t) \tag{3.24}$$

$$= \int_{a_m}^{A_m} \frac{Q_0(a) n_0^*}{1 + n_0^* \pi(a)} da - n_0^* \tag{3.25}$$

$$+\,\varepsilon\left(\int_{a_m}^{A_m}\left(\frac{Q_0p_1(t-a)}{(1+n_0^*\pi(a))^2}+\frac{n_0^*Q_1(a)f(a,t)}{1+n_0^*\pi(a)}\right)da-p_1(t)\right) \tag{3.26}$$

$$\begin{aligned}+\,\varepsilon^2\Bigg(\int_{a_m}^{A_m}\Bigg(&\frac{Q_0p_2(t-a)}{(1+n_0^*\pi(a))^2}-\frac{Q_0(a)p_1(t-a)^2\pi(a)}{(1+n_0^*\pi(a))^3}\\&+\frac{Q_1(a)f(a,t)p_1(t-a)}{(1+n_0^*\pi(a))^2}\Bigg)da-p_2(t)\Bigg)\end{aligned} \tag{3.27}$$

$$\begin{aligned}&+\,\varepsilon^3\Bigg(\int_{a_m}^{A_m}\frac{\pm CQ_0(a)}{(1+n_0^*\pi(a))^2}da\mp C\\&+\int_{a_m}^{A_m}\frac{Q_0(a)}{1+n_0^*\pi(a)}\left(\frac{p_1^3(t-a)\pi^2(a)}{(1+n_0^*\pi(a))^3}-\frac{2p_1(t-a)p_2(t-a)\pi(a)}{(1+n_0^*\pi(a))^2}\right)da\\&+\int_{a_m}^{A_m}\frac{Q_1(a)f(a,t)}{1+n_0^*\pi(a)}\left(\frac{p_2(t-a)}{1+n_0^*\pi(a)}-\frac{p_1^2(t-a)\pi(a)}{1+n_0^*\pi(a)}\right)da\Bigg)+O(\varepsilon^4).\end{aligned} \tag{3.28}$$

We will now prove that the terms (3.24), (3.26) and (3.27) are zero. By the definition of $n_0^*$ we have that (3.24) is zero. Next we study the second term (3.26). We have

$$\int_{a_m}^{A_m}\left(\frac{Q_0p_1(t-a)}{(1+n_0^*\pi(a))^2}+\frac{n_0^*Q_1(a)f(a,t)}{1+n_0^*\pi(a)}\right)da-p_1(t).$$

Expressing $p_1(t)$ and $f(a,t)$ with sums we get

$$\begin{aligned}&=\int_{a_m}^{A_m}\left(\frac{Q_0\sum\limits_{n=-N}^{N}a_nb(nA)e^{inA(t-a)}}{(1+n_0^*\pi(a))^2}+\frac{n_0^*\sum\limits_{n=-N}^{N}a_ne^{inAt}Q_1(a)}{1+n_0^*\pi(a)}\right)da\\&\qquad-\sum_{n=-N}^{N}a_nb(nA)e^{inAt}\\&=\sum_{n=-N}^{N}a_ne^{int}\left(\int_{a_m}^{A_m}\frac{Q_0b(nA)e^{-iAna}}{(1+n_0^*\pi(a))^2}+\frac{n_0^*Q_1(a)}{1+n_0^*\pi(a)}da-b(nA)\right)=0.\end{aligned}$$

Since this must hold for every $t$ we get:

$$b(nA)=\frac{\int_{a_m}^{A_m}\frac{n_0^*Q_1(a)}{1+n_0^*\pi(a)}da}{1-\int_{a_m}^{A_m}\frac{Q_0e^{-inAa}}{(1+n_0^*\pi(a))^2}da}. \tag{3.29}$$

Next we study 3.27. We have

$$
\begin{aligned}
&\int_{a_m}^{A_m} \left( \frac{Q_0 p_2(t-a)}{(1+n_0^*\pi(a))^2} - \frac{Q_0(a)\left(p_1(t-a)\right)^2 \pi(a)}{(1+n_0^*\pi(a))^3} \right. \\
&\qquad \left. + \frac{Q_1(a) f(a,t) p_1(t-a)}{(1+n_0^*\pi(a))^2} \right) da - p_2(t) \\
&\quad = \int_{a_m}^{A_m} \left( \frac{Q_0 \left( k_2 + \sum\limits_{n_1=-N}^{N} \sum\limits_{n_2=-N}^{N} c_{n_1,n_2} e^{iA(n_1+n_2)(t-a)} \right)}{(1+n_0^*\pi(a))^2} \right. \\
&\qquad \left. - \frac{Q_0(a) \left( \sum\limits_{n_1=-N}^{N} \sum\limits_{-N}^{N} a_{n_1} a_{n_2} b(n_1 A) b(n_2 A) e^{iA(n_1+n_2)(t-a)} \pi(a) \right)}{(1+n_0^*\pi(a))^3} \right) da \\
&\qquad + \int_{a_m}^{A_m} \frac{\left( \sum\limits_{n=-N}^{N} a_n e^{int} Q_1(a) \right) \left( \sum\limits_{n=-N}^{N} a_n b(nA) e^{inA(t-a)} \right)}{(1+n_0^*\pi(a))^2} da \\
&\qquad - \left( k_2 + \sum_{n_1=-N}^{N} \sum_{n_2=-N}^{N} c_{n_1,n_2} e^{iA(n_1+n_2)(t)} \right) = \\
&= k_2 \int\limits_{a_m}^{A_m} \frac{Q_0(a)}{(1+n_0^*\pi(a))^2} da \left( a_n a_{-n} b(nA) b(-nA) \int\limits_{a_m}^{A_m} \frac{Q_0(a)\pi(a)}{(1+n_0^*\pi(a))^3 da} \right) \\
&\qquad + \int\limits_{a_m}^{A_m} \frac{\sum\limits_{n=-N}^{N} a_n a_{-n} b(-nA)}{(1+n_0^*\pi(a))^2} da - k_2 \\
&\qquad + \sum_{\{(n_2,n_1):n_1+n_2\neq 0\}} e^{i(n_1+n_2)t} \left( \int\limits_{a_m}^{A_m} \left( \frac{Q_0(a) c_{n_1,n_2} e^{-iA(n_1+n_2)a}}{(1+n_0^*\pi(a))^2} - \right. \right. \\
&\qquad - \frac{Q_0(a) a_{n_1} a_{n_2} b(n_1 A) b(n_2 A) e^{-iA(n_1+n_2)a} \pi(a)}{(1+n_0^*\pi(a))^3} \\
&\qquad \left. \left. + \frac{a_{n_1} a_{n_2} b(n_2 A) e^{-iAn_2 a} Q_1(a)}{(1+n_0^*\pi(a))^2} \right) da - c_{n_1,n_2} \right) = 0.
\end{aligned} \tag{3.30}
$$

Which implies that

$$k_2 = \frac{2\sum_{n=1}^{N} a_n a_{-n}\left(b_n b_{-n}\int\limits_{a_m}^{A_m} \frac{Q_0(a)\pi(a)}{(1+n_0^*\pi(a))^3} - \frac{Q_1(a)Re(b(-nA)e^{inAa})}{(1+n_0^*\pi(a))^2}da\right)}{\int\limits_{a_m}^{A_m} \frac{Q_0(a)}{(1+n_0^*\pi(a))^2}da - 1}.$$

Furthermore we can for example choose $c_{n_1,n_2}$ to be

$$c_{n_1,n_2} = \frac{a_{n_1}a_{n_2}\int\limits_{a_m}^{A_m} \frac{Q_0(a)b_{n_1}b_{n_2}e^{-i(n_1+n_2)Aa}\pi(a)}{(1+n_0^*\pi(a))^3} - \frac{b_{n_2}e^{-in_2Aa}Q_1(a)}{(1+n_0^*\pi(a))^2}da}{\int\limits_{a_m}^{A_m} \frac{Q_0(a)e^{-(n_1+n_2)Aa}}{(1+n_0^*\pi(a))^2}da - 1} \tag{3.31}$$

This will satisfy Equation (3.30). Next we study (3.28):

$$\int_{a_m}^{A_m} \frac{\pm CQ_0(a)}{(1+n_0^*\pi(a))^2}da \mp C \tag{3.32a}$$

$$\begin{aligned} &+\int_{a_m}^{A_m} \frac{Q_0(a)}{1+n_0^*\pi(a)}\left(\frac{p_1^3(t-a)\pi^2(a)}{(1+n_0^*\pi(a))^3} - \frac{2p_1(t-a)p_2(t-a)\pi(a)}{(1+n_0^*\pi(a))^2}\right)da \\ &+\int_{a_m}^{A_m} \frac{Q_1(a)f(a,t)}{1+n_0^*\pi(a)}\left(\frac{p_2(t-a)}{1+n_0^*\pi(a)} - \frac{p_1^2(t-a)\pi(a)}{1+n_0^*\pi(a)}\right)da \end{aligned} \tag{3.32b}$$

We now take a look at the term $(3.32a)$. Since by the definition of $n_0^*$ we have

$$\int\limits_{a_m}^{A_m} \frac{Q_0(a)}{1+n_0^*\pi(a)}da = 1$$

and since

$$\frac{1}{1+n_0^*\pi(a)} < 1$$

We have that the term (3.32a) is unbounded and strictly monotonic with respect to $C$. We can also see that the last two terms $(3.32b)$ are bounded. We can now deduce that the last term in our Maclaurin series (3.28) is negative for sufficiently large $C$ in the $n^+(t)$ case and positive for sufficiently large $C$ in the $n^-(t)$ case. This in turn mean that if $\varepsilon$ is small enough (3.19) will be satisfied. According to Theorem 3.1.2 the claim is thereby proved. □

## 3.4 Conclusion

From Theorem (3.2.1) we see that the long term impact of the periodic term is decided by $k_2$ and that the impact growths quadratically with the amplitude $\varepsilon$. Furthermore the impact of each frequency term of $\varepsilon g(t)$ that is $\varepsilon^2 k_2^*$ where $k_2^*$ is defined by (3.18) is added to get the total contribution to the population size $\varepsilon^2 k_2$. If $k_2^*(nA)$ is negative we get a negative contribution to the population size. If on the other hand $k_2^*(nA)$ is positive we get a positive contribution to the population size. In the appendix there are data on four different population histories. For each population in the appendix there are graphs of $k_2$ as a function of $A$ as well as $T = \frac{2\pi}{A}$. From the graphs we can see that the sign of $k_2$ varies with $A$. Unlike the case in the linear model, $k_2(A)$ doesn't converge to zero as $A$ goes to infinity. Instead it appears that as $A$ increases $k_2(A)$ stops changing sign after some point.

## 3.5 Generalisation to infinite fourier series

If we want to generalise Theorem 3.2.1 to the case where $N = \infty$ we only have to assure ourself that every sum in the proof converges. Every sum converges if and only if the sums $f(t) = \sum_{n=-\infty}^{\infty} a_n e^{inAt}$ and $p_1(t) = \sum_{n=-\infty}^{\infty} a_n b(nA) e^{inAt}$ converges. In that case every other sum will converge as well. By definition $g(t)$ does converge. Since $b(nA) \to 1$ at a rate of $\frac{1}{n}$ we can suspect that $p_1(t)$ will converge as well. In fact a sufficient requirement is that $g \in L_T^1$. Then $a_n \to 0$ at a rate of at least $\frac{1}{n}$. Then we have

$$\begin{aligned}
&\sum_{n=-\infty}^{\infty} a_n e^{inAt} - \sum_{n=-\infty}^{\infty} a_n e^{inAt}(1 - b_n) \\
&\quad = \sum_{n=-\infty}^{\infty} (a_n e^{inAt} - (a_n e^{inAt} - a_n b_n e^{inAt})) \\
&\quad = \sum_{n=-\infty}^{\infty} a_n b_n e^{inAt}
\end{aligned}$$

where the left hand side is convergent, which implies that the right hand side is as well.

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# Appendix

## Deriving the interpretation of $e^{-\int_0^a \mu(v,v+t-a)dv}$.

Lets consider the case where we have an individual born at time $(t-a)$ Accordning to Equation (2.1) the distribution $n(v,v+t-a)$ drops by

$$\mu(v,v+t-a)n(v,v+t-a)dv$$

during the infinitesimal time $dv$. So the chance of the individual surviving during the time $dv$ is $1-\mu(v,v+t-a)dv$. Now assuming $\frac{a}{dv}$ is a whole number, if the individual is to survive from birth until age $a$ it has to survive a number of $\frac{a}{dv}$ such moments each with probability

$$1-\mu(v+n*dv,v+n*dv+t-a)dv \quad n=0,1,2\ldots\frac{a}{dv}$$

which has a probability of

$$\prod_{n=0}^{\frac{a}{dv}} 1-\mu(v+n*dv,v+n*dv+t-a)dv$$

Taking the limit as $dv \to 0$ in a way such that $\frac{a}{dv} \in \mathbb{N}$ for every $dv$ we get

$$\begin{aligned}
&\lim_{dv\to 0}\prod_{n=0}^{\frac{a}{dv}} 1-\mu(v+n*dv,v+n*dv+t-a)dv \\
&=\lim_{dv\to 0} exp\left(ln\left(\prod_{n=0}^{\frac{a}{dv}} 1-\mu(v+n*dv,v+n*dv+t-a)dv\right)\right)
\end{aligned}$$

$$= \lim_{dv \to 0} exp\left(\sum_{n=0}^{\frac{a}{dv}} ln\left(1 - \mu(v + n * dv, v + n * dv + t - a)dv\right)\right)$$

$$= /e = \lim_{h \to 0}(1+h)^{\frac{1}{h}}/=$$

$$= \lim_{dv \to 0} exp\left(\sum_{n=0}^{\frac{a}{dv}} ln\left(e^{\mu(v+n*dv, v+n*dv+t-a)dv}\right)\right)$$

$$= e^{\int_0^a \mu(v+n*dv, v+n*dv+t-a)dv}$$

Table 4.1: Life histories

| | Ursus | | Calidris | | Ectotherm | | Insect | |
|---|---|---|---|---|---|---|---|---|
| Age class | s | m | s | m | s | m | s | m |
| 1 | 0,67 | 0 | 0,32 | 0 | 0,13 | 0 | 0,54 | 0 |
| 2 | 0,75 | 0 | 0,78 | 1 | 0,2 | 1 | 0,52 | 0 |
| 3 | 0,82 | 0 | 0,72 | 1 | 0,17 | 30 | 0,49 | 0 |
| 4 | 0,9 | 0,5 | 0,66 | 1 | 0,14 | 30 | 0,47 | 0 |
| 5 | 0,86 | 0,5 | 0,6 | 1 | 0,11 | 30 | 0,45 | 0 |
| 6 | 0,82 | 0,5 | 0,54 | 1 | 0,09 | 30 | 0,42 | 0 |
| 7 | 0,78 | 0,5 | 0,48 | 1 | 0,06 | 30 | 0,4 | 0 |
| 8 | 0,74 | 0,5 | 0,42 | 1 | 0,03 | 30 | 0,38 | 83,33 |
| 9 | 0,7 | 0,5 | 0,36 | 1 | 0,01 | 30 | 0,36 | 166,67 |
| 10 | 0,65 | 0,5 | 0,3 | 1 | 0 | 30 | 0,34 | 250 |
| 11 | 0,61 | 0,5 | 0,24 | 1 | | | 0,32 | 333,33 |
| 12 | 0,57 | 0,5 | 0,18 | 1 | | | 0,3 | 416,67 |
| 13 | 0,53 | 0,5 | 0,12 | 1 | | | 0,27 | 500 |
| 14 | 0,49 | 0,5 | 0,06 | 1 | | | 0,25 | 433,33 |
| 15 | 0,45 | 0,5 | 0,01 | 1 | | | 0,23 | 400 |
| 16 | 0,41 | 0,5 | 0 | 1 | | | 0,21 | 366,67 |
| 17 | 0,37 | 0,5 | | | | | 0,19 | 333,33 |
| 18 | 0,33 | 0,5 | | | | | 0,17 | 300 |
| 19 | 0,29 | 0,5 | | | | | 0,15 | 266,67 |
| 20 | 0,25 | 0,5 | | | | | 0,13 | 233,33 |
| 21 | 0,21 | 0,5 | | | | | 0,11 | 200 |
| 22 | 0,16 | 0,5 | | | | | 0,09 | 166,67 |
| 23 | 0,12 | 0,5 | | | | | 0,06 | 133,33 |
| 24 | 0,08 | 0,5 | | | | | 0,04 | 100 |
| 25 | 0,04 | 0,5 | | | | | 0,02 | 66,67 |
| 26 | 0,01 | 0,5 | | | | | 0,01 | 33,33 |
| 27 | 0 | 0,5 | | | | | | |

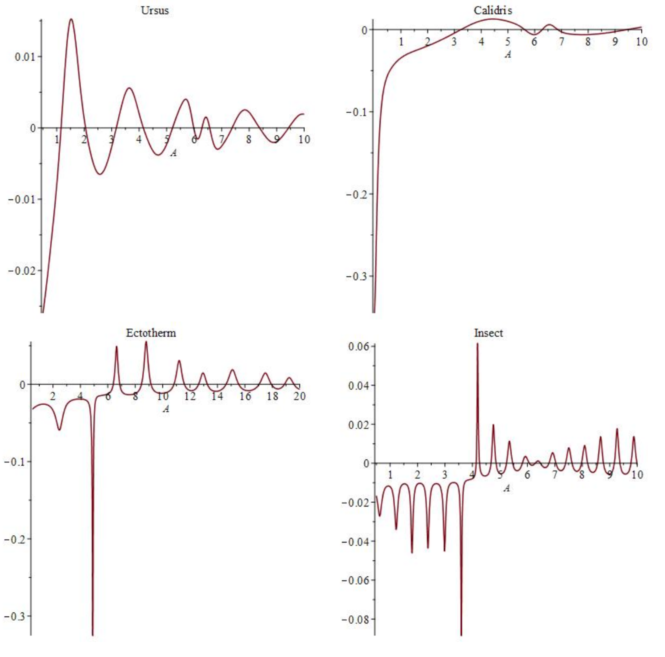


Figure 4.1: $k_2(A)$ (Linear model)

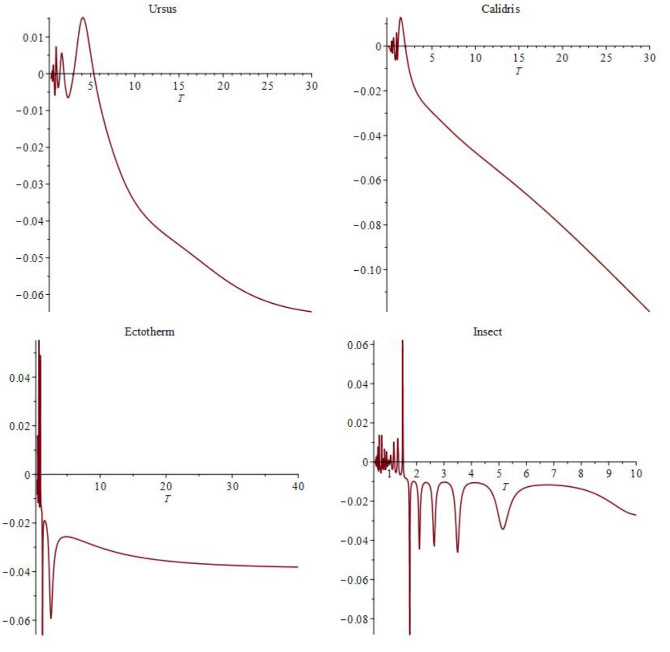


Figure 4.2: $k_2(\frac{2\pi}{T})$ (Linear model)

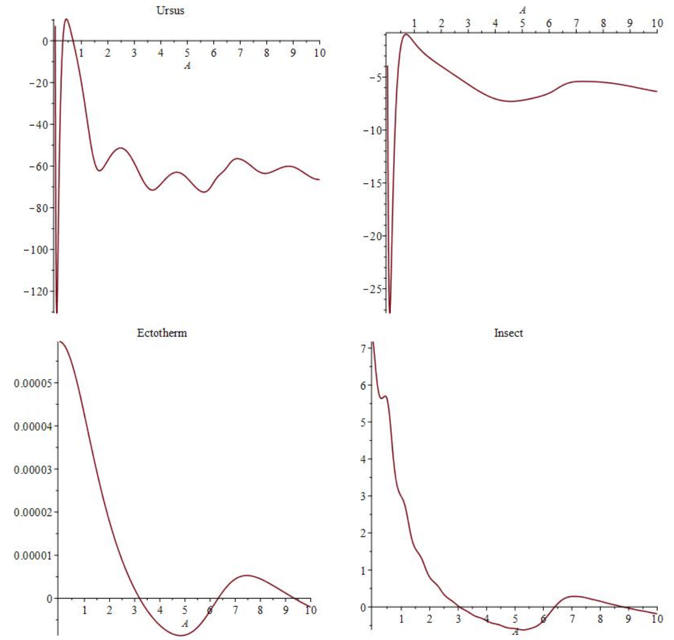


Figure 4.3: $k_2(A)$ (Logistic model)

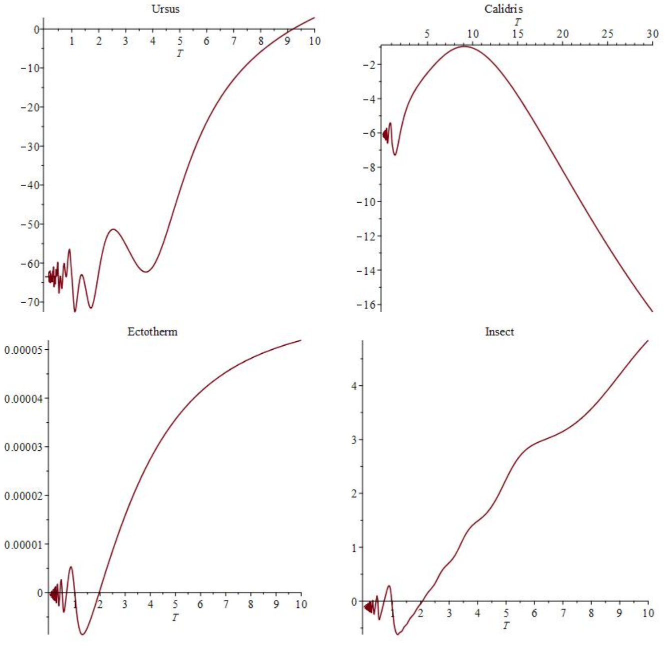


Figure 4.4: $k_2(\frac{2\pi}{T})$ (Logistic model)