

A Model for Arctic Charr Populations in Cambridge Bay
Considering Fluctuating Environment

by

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Abstract

The research focus in this thesis is twofold. First, we formulate an age- and stage-structured discrete-time matrix population model to describe the behaviour of an Arctic Charr population. Given the properties of the model, a weak ergodic behaviour is expected in the long run. Then, utilizing data collected in Cambridge Bay and using a generalized weighted least squares method, model parameters are estimated. The results of estimated parameters and a sensitivity analysis reveal the importance of early-ages individuals in the limiting behaviour of the population.

Second, we investigate how the fitness of such a population might change in a fluctuating environment. We assume three types of yearly environments; good, intermediate and bad. A discrete time Markov chain governs the transitions between environmental states. The results in this step also suggest a weak ergodic behaviour for the population; a stochastic growth rate is provided for the population in this fluctuating environment.

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Chapter 1

Introduction

1.1 Historical importance

Arctic Charr is a Teleostean¹ of the Salmonid² Taxon. They are distributed across the Canadian Arctic Ocean. Over the past 5000 to 6000 years, there has been a strong relationship between Arctic Charr and humans, from subsistence use by Arctic indigenous people to commercial harvest and exportation around the world. Traditionally, the Arviligjuarmiut Inuit of the Canadian central Arctic lived on fishing, hunting and sealing over winter and summer. High accessibility to coastlines, where Arctic Charr live, make Arctic Charr the most important harvest; it represents more than half of Inuit food [1]. Economic developments during the past 50 years have brought enormous changes to the Canadian Arctic residents life style, with Inuit shifting from hunting to grocery shopping as the primary food source [37]. As a result, traditional Arctic Charr harvesting did not continue, but instead commercial fishing started in the late 1940s, when the Shaw Steamship Company harvested a large amount of wild Arctic Charr using gill-nets. The total annual volume of wild population harvesting has been controlled and decreased to 120 tonnes in 2000 [29] (see Table 1.1).

¹In the Teleost order, the largest class of fish make up 96% of all fish.

²Any of various fishes of the family Salmonidae, including salmon, trout, grayling and whitefish.

	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
NWT	—	—	52	62	63	73	53	84	65	60
Labrador	253	243	179	148	142	114	147	95	105	106
Total Canada	—	—	231	210	205	187	201	179	170	166

	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
NWT	43	41	64	130	138	—	—	—	—	—
Labrador	79	84	48	44	33	11	31	37	50	120
Total Canada	122	125	112	174	171	—	—	—	—	—

Table 1.1: Commercial catch from the wild fishery of the Arctic Charr in Canada. Data from [29].

1.2 Recent climate change in the Arctic

Arctic regions are undergoing rapid and severe climatic change, including air temperature warming rates that are greater than the global average [22, 30, 46]. In the last decade, recorded temperatures revealed that the planet has been experiencing average temperature 4°C warmer than the mean temperatures documented from 1951-2000 [46]. These changes are expected to accelerate climate change contributions to major physical, ecological, social and economic changes. More importantly, climate change in the Arctic will also affect the rest of world through increased global warming and rising sea levels.

1.3 Freshwater species are more vulnerable to climate change

Freshwater biodiversity is disproportionately at risk on a global scale, because while fresh waters cover only 0.8% of the Earth's surface, they are home to an estimated 6% of approximately 1.8 million species [11]. Gradual warming may affect fishes in two opposite manners. The consequences may appear positive as warming may result in rapid fish growth rates [51]; however, warming may also lead to lower survival rates since there always is a threshold temperatures for survival which is different between

species.

1.4 Negative effect of global warming on Arctic Charr

Slight differences between summer and winter lake temperature in northern Arctic regions shrink significantly the optimal thermal ranges of species in this region, such as Arctic Charr, which are even more sensitive than their southern relatives [53]. Indeed, Mortensen et. al [47] found that the optimal difference between summer and winter temperature for northern Arctic Charr is about 3°C. Although temperature ranges are species specific, a large increase in water temperature will lead to stress and even mortality in fish population; in the case of sudden changes it has been shown that even gradual increases could eventually be lethal [43, 53].

1.5 Research objective

The overall objective of this thesis is to study the long term dynamics of a model of an Arctic char population in Cambridge Bay (Nunavut) in the presence of water temperature variability.

1.6 Steps of approach

The problem will be studied in two steps. In the first step of the present study, a mathematical model is formulated based on the biological description of the Arctic Charr life-cycle. Given the complicated life-cycle of the species, stage- and age-structure are considered, so that individuals belong to one stage and one age group at the same time. The stage-structure is based on age, physical development and other morphological properties of Arctic Charr.

Some initial mathematical and biological assumptions are made, including constant sex ratio close to 1 : 1 and equal fecundity for all reproducing individuals regardless of their age. A Lefkovich matrix model is implemented to present the age-stage struc-

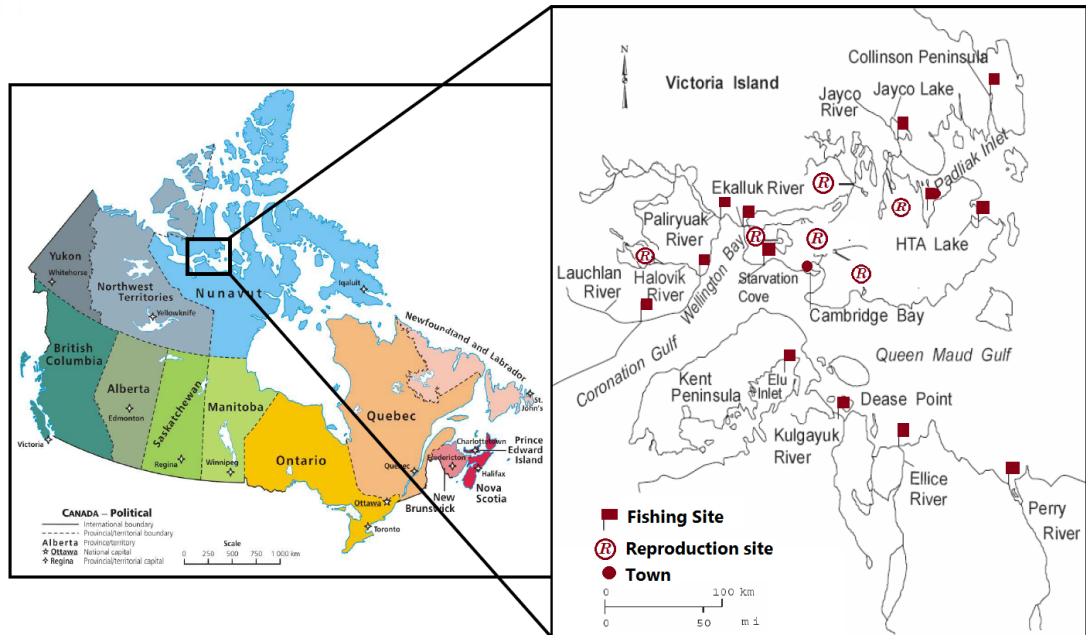


Figure 1.1: Data collection sites map; Cambridge Bay, Nunavut, Canada.

tured population of Arctic Charr. Parameter estimation is conducted based on 39 years of historical data on the population of Arctic Charr, which was collected by Fisheries and Oceans Canada from fishing sites located at the mouths of 6 rivers on Cambridge Bay: Lauchlan, Halovik, Paliryuak, Ekallik, Ellice and Jayco (Figure 1.1). Given the stage structure of the population and the relation between sub-populations, a weighted least square method is utilized in order to estimate parameters of model.

In the second step, we investigate how the occurrence of favourable, neutral and unfavourable years in a random sequence could affect the fitness of the population in the long run. We classify years into these three categories according to our knowledge of how Arctic Charr responds biologically to different climate states in the important months of a year. It is supposed that switching between good, intermediate and bad years is governed by a Markov random process. Given the randomness of Markov chain draws, which represent transitions between the three types of years, the current study involves non-homogeneous products of matrices formed by three fixed transition matrices corresponding to the aforementioned three classes of years. The stochastic growth rate is calculated. Moreover, the ergodic behaviour of the population in the presence of fluctuating environments is discussed.

Chapter 2

Literature review

2.1 Biological background

Wild Arctic Charr are distributed along the seashore regions in Canada's High Arctic, Greenland, Iceland, northern Scandinavia, Russia and around the many small islands located at the edges of Arctic seas. They are anadromous, i.e., in some stages of their life they immigrate from fresh water to sea during the short Arctic summer, reserving energy for a long winter famine and reproducing when they return to freshwater lakes or rivers in the fall [29].

2.1.1 Taxonomy and geographic distribution

The taxonomic status of Arctic Charr was not conclusively stated within the Salmonid subfamily until lately. In [24], using a type specimen from Swedish Lapland [56], this species was officially named Arctic Charr and classified as a Salmonid species. However, there are in fact many species of the Arctic Charr type. In the Canadian High Arctic region of Nunavut, Arctic Charr are observed as the only salmonid species [29] and in some freshwater niches such as Lake Hazen on Ellesmere Island and Charr Lake near Resolute Bay, this kind of fish is recorded as the only fish [44, 52]. Arctic Charr are also one of the most adaptable Arctic fishes [29], in the sense of finding food and high adaptability to the harsh northern environment (Figure 2.1).

2.1. BIOLOGICAL BACKGROUND

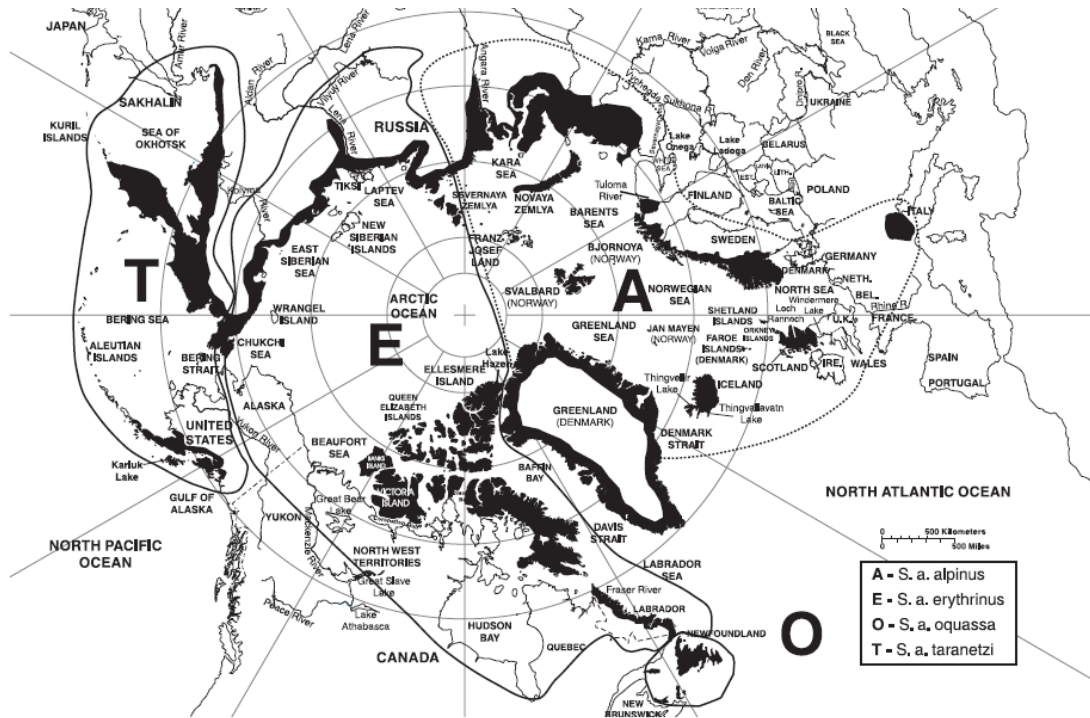


Figure 2.1: Circumpolar distribution of wild Arctic Charr [29].

For North American Charr, two different ancestries are proposed [66]: one from a northern glacial refugia¹ and an eastern Laurentian lineage from an eastern glacial refugia in which these two probably diverged about 1–1.6 million years ago. Diversity in geographic dispersal has led to delicate differences in morphological characteristics such as body size at maturity, flesh colour and age at maturity.

Two general life-history patterns of Arctic Charr are suggested among all the aforementioned subspecies [29]: Anadromous and Resident forms. The first group spends a brief part of their lifetime in the ocean accessing food resources there, then return to fresh water at the end of summer; the second group may spend their entire life-time in the fresh water environments of lakes or rivers. Regardless of having different life-cycles, both anadromous and resident Arctic Charr may co-exist in some regions [29].

¹Refugia (singular Refugium) are geographical locations where natural environmental conditions have remained relatively constant or stable during times of great environmental change, such as eras of glacial advance and retreat. [48]

2.1. BIOLOGICAL BACKGROUND

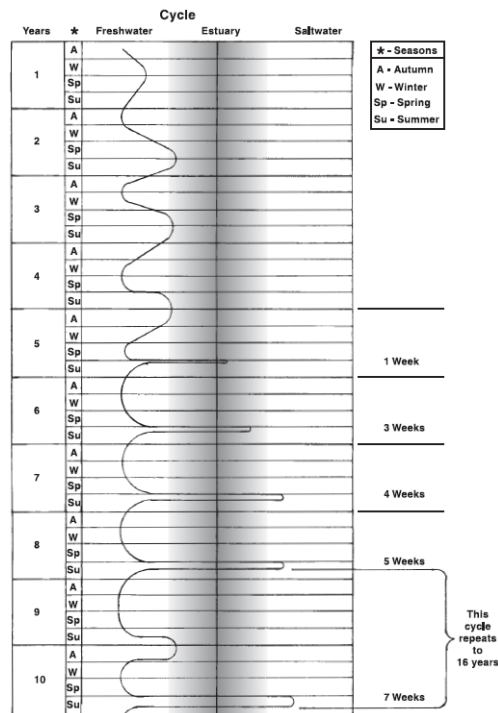


Figure 2.2: Relative amount of time Arctic Charr of different ages spend in fresh water and sea [29].

2.1.2 Anadromous Arctic Charr life-cycle

The focus of the current study is on the anadromous form of Arctic Charr. This species is born in streams, where they start their growth. After several years spent only in rivers, individuals undertake a summer migration to the sea where they feed from the rich available marine food resources. In order to handle the large difference of water temperature between river and sea, they need to be at least 15 cm in length, so in addition to age, their body size is considered as an important factor in their ability to migrate [29]. Arctic Charr individuals can be observed in sea water starting mid-to-late June, when the sea water temperature rarely rises to 10°C. Between mid August to early September, when the water temperature is near to 0°C, they return to rivers. Their fidelity to birth river seems high especially in reproducing years; about 70% of new residents of rivers are those who migrated from the same river at the beginning of summer and only 30% are migrants from other rivers [29]. Despite undertaking several migrations during their life-cycle, anadromous Arctic Charr spend less than 15% of their lifetime in the sea (Figure 2.2).

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	Weight			Length		
	SGR(%)	Days	Growth(%)	SGR(%)	Days	Growth(%)
Summer feeding						
Maximum	2.05	37*	75	0.34	37*	13
Average	1.55	44*	68	0.31	44*	14
Minimum	1.23	45*	74	0.25	60*	15
Winter fasting						
Maximum	-0.01	320	-4	0.02	321	7
Average	-0.04	315	-12	0.01	315	6
Minimum	-0.11	293	0.01	0.01	293	3

Table 2.1: Differences in growth rate between summer feeding and winter fasting in anadromous Arctic Charr. (SGR = specific growth rate) Source: [2, 29].

Stock	Age at Maturity	Size at maturation	
		Weight(g)	Length(cm)
Nauyuk Lake	10	3415	620
Baffin*	16	2050	600
Creswell Bay*	13	2047	570
Tree River*	8		500
Ellesmere*	16	850	463
Sylvia Grinnel*	14	1950	450
Mackinson Inlet*	12	925	447
Cumberland*	11	615	400
Fraser River*	5		262

Table 2.2: Age and size at maturity of anadromous Arctic Charr. Source: [2, 28, 29, 35].
* The data related to these rivers is not included in the present study.

Two distinct phases are introduced in [29] for the growth of the wild Arctic Charr population. The first phase happens during the 40 to 60 days stay in the sea habitat in which high access to rich food resources and favourable water temperature offer a daily growth rate of sometimes more than 2% [29]. The second phase is the slow growth which happens during the harsh winter and while staying in rivers. A similar pattern for the rate of growth of body length is suggested in [29]. Fish body length is an important index of maturity, even more important than chronological age [2]. The age at maturity is usually 5 years, though it varies based on the location (Table 2.2).

Once an individual moves to the mature stage, it is able to reproduce up to the age of 20; this species can live for 30 to 40 years [29]. Most anadromous Arctic Charr

2.1. BIOLOGICAL BACKGROUND

cannot spawn yearly; they usually skip one to three years to fully recover and gain enough weight (a reproducing female loses from 30% to 40% of its body mass [12]). Arctic Charr spawn in near-shore lake shoals and in streams and rivers. In Northern Canada, they spawn from late August to late September [56]. Water temperature is low in spawning areas, between 0.5 and 7°C. The number of eggs produced increases with body size and the maximum number is estimated between 3000 and 5000 eggs per individual. Eggs laid in September hatch after about 60 to 230 days in late March or early April; during this time, water temperature is about 0.75 to 1.5°C. The length of the incubation period is highly related to the water temperature; it decreases from 97 days at 4°C to 36 days at 12°C. However, some experiments reveal that egg mortality increases above 7°C and increases extremely at 14°C, so there always is a trade off between growth rate and survival rates [29]. Arctic Charr, especially in Northern countries, tolerate a vast range of temperature but generally prefer mean water temperature below 15°C. Also, they consume a wide range of foods which helps them survive the long winter in rivers, where food resources are very limited. Despite the high resistance of Arctic Charr to low water temperatures, one of the reasons of growth rate fluctuations is still the water temperature. The optimum temperature for Arctic Charr varies considerably for different ages and stages. Cold water, from 2 to 7°C, is required for egg production and incubation (a few weeks before fertilization and a couple of weeks after the eggs turn into eyed fish²), while the highest growth rate for the juvenile stage is reported at 13 to 18°C [27, 38, 59]. Transition from the immature to the mature stage happens between 10 to 15°C and the highest growth rate for mature wild Arctic Charr is about 1% per day and happens in the sea environment when the water temperature varies between 0.5 and 4°C. The upper bound for growth and feeding is reported as 21.5°C and temperature above 23°C are lethal for mature individuals [5] (Figure 2.3).

Moreover, in [64] it is shown that the food conversion rate is maximum at 9°C and

²In [28] the Arctic Charr life cycle is introduced in 5 different stages; embryonic, alevin, juvenile, adult and senescent. The first stage itself has 10 different steps of physical developments. The term *eyed* refers to one of these development steps when the egg has developed enough that the black spot of the eyes are visible through the egg membrane [15].

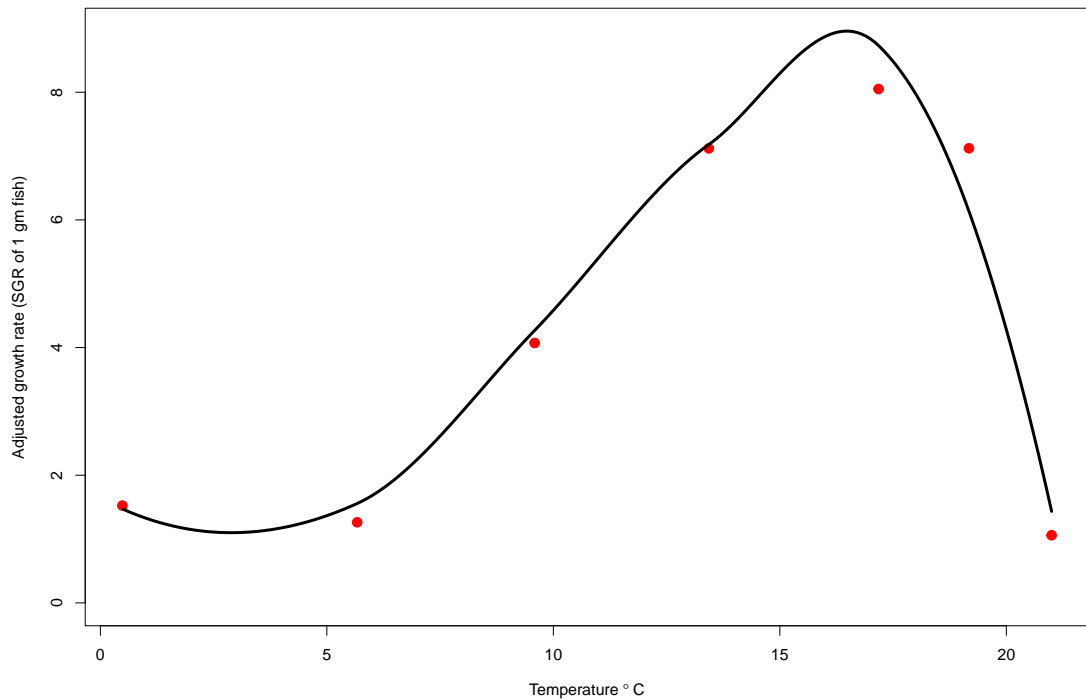


Figure 2.3: Effect of water temperature on growth rates of Arctic Charr (data source [29]).

there is a negative linear relation between this rate and water temperature. Also, there exists a strong relation between water temperature and the chemical parameters of the water (oxygen, carbon dioxide, pH, ammonia-N, ...) and the risk of different water diseases which could affect both survival and important events in the Arctic Charr life-cycle (Figure 2.4).

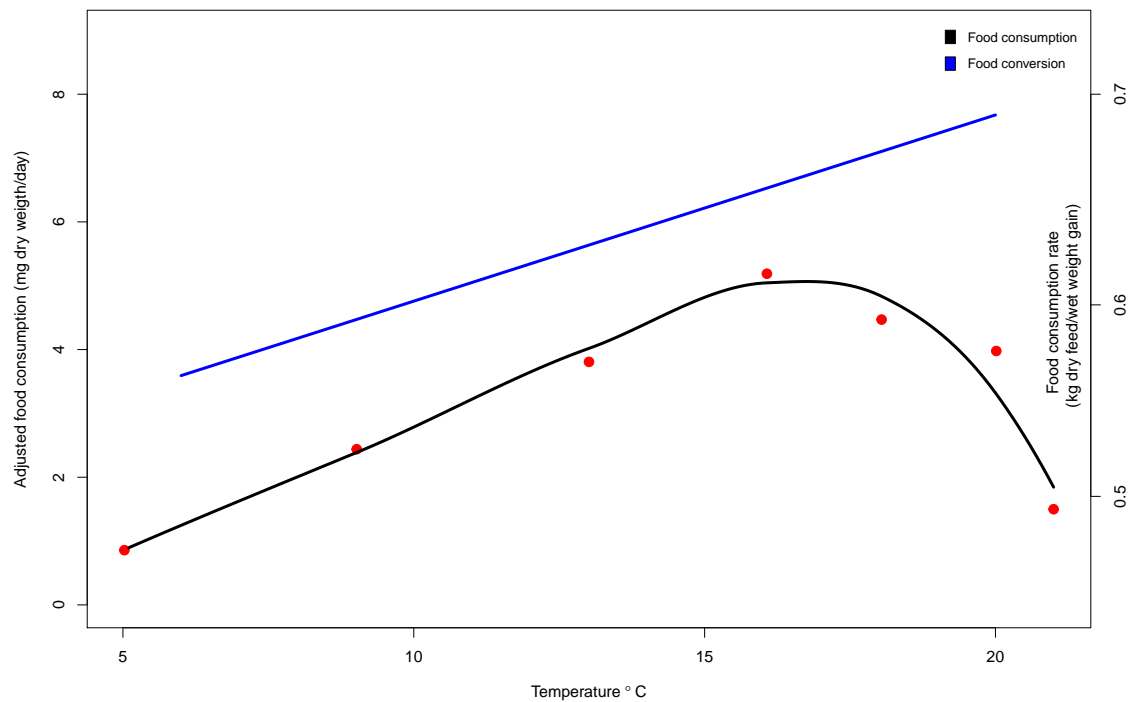


Figure 2.4: Effect of temperature on food consumption and food conversion rates (Data source [26, 28]).

2.2 Mathematical background

A mathematical model that describes the distribution of individuals given the existence of different categories of individuals is called structured model. For instance, in some populations, age differences are the most important factor, while in some others, size distribution or physical development stages provide a better description. For some populations, it may be necessary to classify by more than one characteristic such as age and size or age and development stages [7, 63]. A structured model reflects the dynamics of individuals during their lifetime. A basic classification of mathematical approaches to representing the dynamics of structured populations in [62] lists three main methods: Matrix models, Delay Differential Equation models and Partial Differential Equation models. Because matrix models are used here, these models are now briefly presented.

2.2.1 Matrix models

Considering a discrete-time framework, in a matrix model the population should be classified into discrete categories (such as age, stage of physical development, size, sex, ...) in which a vector $\mathbf{n}(t) = [n_1(t), \dots, n_k(t)]^T$ represents a population with k classes at time t . A transition matrix A contains the probabilities of transitions between states. To project the population from time $t_0 + (t - 1)$ to $t_0 + t$ we have

$$\mathbf{n}(t_0 + t) = A\mathbf{n}(t_0 + (t - 1)). \quad (2.1)$$

Therefore, by starting with an initial population $\mathbf{n}(t_0) = n_0$, we can project the population from time t_0 to $t_0 + 1$ as follows:

$$\begin{aligned} \mathbf{n}(t_0 + 1) &= A\mathbf{n}(t_0) \\ &= An_0. \end{aligned} \quad (2.2)$$

Population projection from time $t_0 + 1$ to $t_0 + 2$ take following form:

$$\begin{aligned} \mathbf{n}(t_0 + 2) &= A\mathbf{n}(t_0 + 1) \\ &= A(An_0) \\ &= A^2n_0. \end{aligned} \quad (2.3)$$

By repeatedly applying the matrix model (2.1) and using the initial population n_0 , we see that

$$\begin{aligned} \mathbf{n}(t_0 + t) &= A\mathbf{n}(t_0 + (t - 1)) \\ &= A^t\mathbf{n}(t_0) \\ &= A^tn_0. \end{aligned} \quad (2.4)$$

Advantages of this model include that it is easy to formulate, rather easy to simulate using matrix multiplications and relatively easy to analyse. On the other hand, assuming a discrete structure for the population, as well as a high sensitivity to the choice of

stages can be considered as restrictions of this type of model.

One of the most famous matrix model for the dynamics of structured populations is called the Leslie model. Leslie matrices were introduced in [40] as follows

- n_{xt} is the number of females alive in the “age group x to $x + 1$ ” at time t (note that age group x to $x + 1$ indicates individuals with ages between x and $x + 1$),
- P_x is the probability that a female aged x to $x + 1$ at time t will be alive in age group $x + 1$ to $x + 2$ at time $t + 1$,
- F_x is the number of daughters born in the interval t to $t + 1$ per female alive aged x to $x + 1$ at time t , who will be alive in the age group 0-1 at time $t + 1$.

Then, working from an origin of time $t_0 = 0$, the age distribution at the end of one unit time interval will be given by:

$$\sum_{x=0}^m F_x n_{x0} = n_{01} \quad (2.5)$$

$$P_0 n_{00} = n_{11} \quad (2.6)$$

$$P_1 n_{10} = n_{21} \quad (2.7)$$

$$P_2 n_{20} = n_{31} \quad (2.8)$$

$$\vdots \quad \vdots \quad (2.9)$$

$$P_{m-1} n_{m-1,0} = n_{m1} \quad (2.10)$$

or, employing matrix notation, $Mn_0 = n_1$, where n_0 and n_1 are column vectors giving the age distribution at t_0 and t_1 respectively, and M is a *projection* matrix given by:

$$M = \begin{bmatrix} F_0 & F_1 & F_2 & \dots & F_k & F_{k+1} & \dots & F_{m-1} & F_m \\ P_0 & 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & P_1 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & P_2 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & \dots & P_k & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & P_{k+1} & \dots & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 & \dots & P_{m-1} & 0 \end{bmatrix}.$$

All elements of M are zero, except those in the first row and in the sub-diagonal immediately below the principal diagonal. Indeed, Leslie [40] classified populations into age groups. However, for some populations, crucial dynamics may happen in different groups of population rather than in their age classes. Therefore, Lefkovich in 1965 [39] replaced equal age groups by unequal stage division of a population; the projection matrix then takes the form:

$$M = \begin{bmatrix} P_1 & F_2 & F_3 & F_4 & \dots & F_{m-1} & F_m \\ G_1 & P_2 & 0 & 0 & \dots & 0 & 0 \\ 0 & G_2 & P_3 & 0 & \dots & 0 & 0 \\ 0 & 0 & G_3 & P_4 & \dots & 0 & 0 \\ 0 & 0 & 0 & \ddots & \ddots & 0 & 0 \\ 0 & 0 & 0 & 0 & \dots & P_{m-1} & 0 \\ 0 & 0 & 0 & 0 & \dots & G_{m-1} & P_m \end{bmatrix},$$

where:

- F_i is the stage-specific fecundity ($i = 1, 2, \dots, m$), where m is the number of stages,
- P_i is the probability of surviving and remaining in stage i (surviving for entire length of stage),

- G_i is the probability of surviving and growing into the next stage class (from stage i to $i + 1$), i.e., the proportion of individuals in the oldest cohort of the stage times the annual survival for the stage.

To evaluate the above quantities we require two further definitions.

- d_i is the duration of sojourn in stage $i = 1, 2, \dots, m$ and p_i is the probability that individuals in the stage survive to the next year but still stay in stage i .

Since the probability of those individuals surviving d years in stage i is p_i^d , the relative abundances of these groups of individuals within stage i are $1, p_i, p_i^2, \dots, p_i^{d-1}$. Thus, the proportion remaining and surviving in the stage i , P_i , is formulated as follows:

$$P_i = \left(\frac{1 + p_i + p_i^2 + \dots + p_i^{d-2}}{1 + p_i + p_i^2 + \dots + p_i^{d-1}} \right) p_i, \quad (2.11)$$

which, using the geometric series formula $1 + p + p^2 + \dots + p^{d-2} = \frac{1-p^d}{1-p}$, given for $i = 1, 2, \dots, m$

$$P_i = \frac{1 - p_i^{d-1}}{1 - p_i^{d_i}} p_i. \quad (2.12)$$

Also, for G_i we have

$$G_i = \left(\frac{p_i^{d-1}}{1 + p_i + p_i^2 + \dots + p_i^{d-1}} \right) p_i, \quad (2.13)$$

which can be written, in the same way as before, as

$$G_i = \frac{P_i^{d_i}(1 - p_i)}{1 - P_i^{d_i}} \quad i = 1, 2, \dots, m - 1. \quad (2.14)$$

It is assumed that once an individual leaves a stage class, it cannot re-enter it later. Later on, in Section 2.2.2, when we discuss matrix model analysis, we use these two types of matrices frequently. First, note a few facts about the eigenvalues and eigenvectors of a matrix.

Eigenvalue of a square matrix

Eigenvalues are special values associated to square matrices. A scalar λ is called an eigenvalue for matrix A and \mathbf{w} and \mathbf{v} are called right and left eigenvectors corresponding to λ , respectively, if they satisfy the following equations:

$$A\mathbf{w} = \lambda\mathbf{w} \tag{2.15a}$$

$$\mathbf{v}^*A = \lambda\mathbf{v}^* \tag{2.15b}$$

where \mathbf{v}^* are respectively the complex conjugate transpose of right and left eigenvectors corresponding to λ .

The eigenvalues of A can be found as solutions of the characteristic equation $\det(A - \lambda I) = 0$, where I is the identity matrix. If A is a $k \times k$ matrix, the characteristic equation is a polynomial of degree k and has k solutions $\lambda_i, i = 1, 2, \dots, k$ (which can take positive, negative or zero, real or complex values). Then, the corresponding right and left eigenvectors to λ_i are denoted w_i and $v_i, i = 1, 2, \dots, k$. A positive (real) eigenvalue λ_1 is called a *dominant eigenvalue* of matrix A if all other eigenvalues λ of A satisfy $|\lambda| \leq \lambda_1$. Later, in the Perron-Frobenius Theorem (Theorem 2.1), we discuss a number of properties of dominant eigenvalues.

Leslie in the 1940's used his model for structured populations but it remained abandoned until the late 1960s when it was rediscovered by ecologists [39] and human demographers [17, 31]. In the 1970s, biologists found matrix models to be a potent tool to describe plant multi-stage life-cycles [21, 54, 65].

2.2.2 Analysis of matrix models

Based on the nature of the population under consideration, there could be different answers to the essential question of what happens in the next projection interval. Three general classes of models exist [62] to describe three different answers to this question, including linear constant-coefficients, non-linear and time-varying models. The first model is applicable if a constant matrix A is considered and the population projection

is formulated as (2.1). Then matrix A can depend on the current state of population (frequency or density dependence); the model is then non-linear and the population projection takes the form:

$$\mathbf{n}(t + 1) = A(\mathbf{n}(t))\mathbf{n}(t), \quad (2.16)$$

where $A(\mathbf{n}(t))$ is the transition matrix evaluated at $\mathbf{n}(t)$. Time-varying models can also be used to explain the dynamic of a population, when the transitions between stages are time dependent. Let $A(t)$ be the transition matrix evaluated at time t , then the population projection is formulated as follows:

$$\mathbf{n}(t + 1) = A(t) \mathbf{n}(t). \quad (2.17)$$

Note that (2.17) includes (2.16) as a particular case.

Different mathematical tools are available to answer three important categories of questions [7, 63].

1. *Transient analyses*

The aim of this type of analysis is to describe the short-term dynamics of structured populations. In linear case, transient dynamics may involve oscillations and can be characterized by the frequency of these oscillations and their rate of decay as the system approaches its long-term attractor. In non-linear case, the dynamics are characterized by the rate of approach to attractors or invariant measures. The dynamics in this case depend on the initial conditions.

2. *Asymptotic analyses*

The main problem here is the description of population behaviour in the long run [7, 63]. To answer this general question, emphasis on four important factors is necessary: the exponential rate of growth, the stable population (age, stage, . . .) distribution, i.e., the asymptotic dynamics of the population, ergodicity (which in most of the structured population literature indicates the convergence to a

stable distribution and may happen after some initial fluctuations) and finally the qualitative properties of the asymptotic dynamics such as fixed points, cycles, etc. which are referred to as attractors.

3. Perturbation analyses

The effects of any perturbation in initial conditions or parameters of a model can be analysed in the sense of the three following factors;

- Sensitivity and elasticity analysis
- Stability analysis
- Bifurcation analysis

2.2.3 Asymptotic analyses in the presence of constant vital rates

Given the importance of asymptotic analyses in the present study, a brief literature review is provided. We begin with some definitions and an important theorem.

Definition 2.1. *A real matrix A is non-negative (or positive) if all the entries of A are non-negative (or positive), which is denoted by $A \geq 0$ (or $A > 0$).*

Definition 2.2. *A non-negative square matrix A is called primitive if there is a p such that all the entries of A^p are positive.*

Definition 2.3. *A non-negative square matrix A is called irreducible if for all i, j , there exists an scalar $k = k(i, j)$ such that the (i, j) entry of A^k , $A_{ij}^k > 0$.*

An interesting result about such matrices is stated in [25] as follows:

Lemma 2.1. *Let A be a non-negative and primitive matrix. Then A^k is non-negative, irreducible and primitive for all $k = 1, 2, \dots$*

Oskar Perron in 1907 [49] developed some fundamental results in the theory of non-negative matrices. He proved the theorem which today is called the Perron-Frobenius Theorem for matrices with positive entries. Ferdinand Georg Frobenius extended the theorem to irreducible and non-negative matrices in 1912 [13]. The

Perron-Frobenius Theorem guarantees the existence of a real dominant eigenvalue for irreducible square matrices and the uniqueness of corresponding left and right eigenvectors corresponding to this dominant eigenvalue.

Theorem 2.1 (Perron- Frobenius). *Suppose $A \geq 0$ is an irreducible square matrix.*

Then

1. *A has a positive (real) eigenvalue λ_1 such that all other eigenvalues λ of A satisfy $|\lambda| \leq \lambda_1$*
2. *λ_1 has algebraic, hence also geometric, multiplicity one and (a suitably scaled version of) the corresponding eigenvector v has strictly positive entries;*
3. *The only non-negative eigenvectors of A are multiples of v ;*
4. *More generally, if $y \geq 0, y \neq 0$ is a vector and μ is a number such that $Ay \leq \mu y$ then $y > 0$ and $\mu \geq \lambda_1$ with $\mu = \lambda_1$ if and only if y is a multiple of v .*

As a result, if A is primitive, then all other eigenvalues λ of A satisfy $|\lambda| < \lambda_1$.

Definition 2.4. *The exponential rate of growth in linear deterministic problems of the form (2.1) is the dominant eigenvalue λ_1 of population-projection matrix A .*

The dominant eigenvalue λ_1 can be used to determine the long term dynamics of the population, i.e., to demonstrate whether the population is increasing, decreasing or constant. Using Matrix model (2.4), we need only understand the behaviour of A^t to better understand population dynamics over time. Based on (2.15), we can write any matrix A of size $k \times k$ with distinct eigenvalues as

$$A = \lambda_1 Z_1 + \lambda_2 Z_2 + \cdots + \lambda_k Z_k, \quad (2.18)$$

where the matrices Z_i are known as *constituent matrices* of A and take the form

$$Z_i = \mathbf{w}_i \mathbf{v}_i^*, \quad (2.19)$$

where \mathbf{w}_i and \mathbf{v}_i are normalized to one. Constituent matrices have two interesting properties. First, they are idempotent, i.e.,

$$Z_i^2 = Z_i, \quad \forall i = 1, \dots, k. \quad (2.20)$$

Second,

$$Z_i Z_j = 0, \quad \forall i, j = 1, \dots, k. \quad (2.21)$$

Using the above properties and (2.18), we have the following equation [62]:

$$A^t = \sum_i \lambda_i^t Z_i. \quad (2.22)$$

Therefore, we can rewrite (2.4) as

$$\mathbf{n}(t_0 + t) = \sum_i \lambda_i^t Z_i \mathbf{n}(t_0). \quad (2.23)$$

where $Z_i \mathbf{n}(t_0)$ are not zero vectors. Since the only parts of the right side of (2.23) that are changing with time are λ_i^t , the behaviour of the population basically depends on the sign and type (real or complex) of dominant eigenvalue of A , λ_1 .

In the case that λ_1 is real and positive, in the long run we expect that the population grows or decays exponentially, depending on whether λ_1 is greater or less than one. For real and negative values the growth rate oscillates between positive and negative values, growing or decaying depending on whether $|\lambda_1|$ is greater or less than one.

If λ_1 is complex, the limiting growth rate oscillates in a sinusoidal pattern, growing or decaying in magnitude depending on whether $|\lambda_1|$ is greater or less than one [62]. Therefore, having different values of λ_1 , we expect different behaviour for the population in the long term. As discussed, the Perron-Frobenius Theorem (Theorem 2.1) provides important information about the sign and type (real or complex) of eigenvalues of irreducible and primitive matrices, guaranteeing an exponential rate of growth given a primitive transition matrix.

Also, the left and right eigenvectors corresponding to the dominant eigenvalue λ_1 contribute to the short-term transient and the eventual dynamics of population [62]. The dominant right eigenvector is the stable stage distribution and the dominant left eigenvector is known as the reproductive-value vector. In fact, it is proved that the population structure eventually becomes proportional to a right eigenvector \mathbf{w}_1 (if the vital rates remain constant) and this proportionality is a weighted sum of the initial numbers in each stage ($\mathbf{v}_1^n(t_0)$), which can be interpreted as the relative contributions of the stages to the eventual population size. More precisely,

$$\lim_{t \rightarrow \infty} \frac{\mathbf{n}(t_0 + t)}{\lambda_1^t} = \mathbf{w}_1 \mathbf{v}_1^* \mathbf{n}(t_0), \quad (2.24)$$

where the vectors \mathbf{w}_1 and \mathbf{v}_1 are the normalized (normalized to one) dominant right and left eigenvectors of A and the asterisk denotes the complex conjugate transpose.

2.2.4 Ergodicity

Lotka in his essential work [42] described how a stable age structure can be generated and determined for an age-structured population which is both isolated from migratory movements and has unchanging age specific fertility and mortality rates. Interestingly, he stressed that this stable structure is independent of the vital rates of birth and death in which the population starts to operate. Inspired by Lotka's contributions to the mathematical theory of human population growth, Lopez [41] concentrated on age structured populations and offered a different and simpler proof for the so-called weak ergodic theorem. In fact, he distinguished between **weak** and **strong ergodicity**; the latter is present when the age structure has a stable asymptotic distribution with assuming constant mortality and fertility rates, while weak ergodicity is described as the tendency of population distributions of different populations to be similar in the long run but without any guarantee of approaching a limiting distribution. Equivalently, the population 'forgets' its age distributions in the remote past when it is strongly ergodic and the direction of population vector approaches a limit when fertility and mortality

are kept unchanged. As a part of this work, [41] used a matrix formulation to model a discrete-time, age-structured population problem, which made it easier to study infinite products of a non-homogeneous³ chain of matrices. He showed that to have a weak ergodic age structure, it is sufficient that the rows of such non-homogeneous products of matrices tend to a similarity (row proportionality 2.25). Doing so, [41] considered some initial assumptions, a number of which were relaxed completely or partially during the study. The important assumptions in [41] are as follows:

1. Only the female population is considered and in the absence of immigration.
2. Age is an integer and varies from zero to a finite value ω .
3. Only ages up to a limiting age of reproduction β are considered.
4. The fertility $f_i^{(t)}$ is defined as the chance that a female of age i at time t will bear a child in the following year who survives to the end of that year; it is assumed that for some $\varepsilon > 0$, either $f_i^{(t)} > \varepsilon$ or $f_i^{(t)} = 0$ for any i and t . Also, for now it is assumed that for all t , $f_\beta^{(t)} > 0$.
5. If for any i and t_k we have $f_i^{(t_k)} > 0$, then $f_i^{(t)} > 0$ for all t , (this assumption is later relaxed).
6. The survival $p_i^{(t)}$ is defined as the probability that a female of age i at time t survives one year later; it is assumed that for all t and $i < \beta$ (β introduced in the above assumption on fertility), $p_i^{(t)} > \varepsilon > 0$. (Note that Lopez in [41] named this value as “mortality”.)
7. $s_i^{(t)}$ and $z_i^{(t)}$ are the age distribution vectors of two different populations at time t , with initial vectors defined as $s^{(t)} = [s_0^{(t)}, s_\beta^{(t)}]$ and $z^{(t)} = [z_0^{(t)}, z_\beta^{(t)}]$. It is assumed that $s_i^{(0)}$ and $z_i^{(0)}$ are strictly positive for every i and there exist positive numbers P and Q such as for every i and j ,

³let $S = \{A_i : A_i \in \mathbf{M}_{n \times n}, i = 1, \dots, m\}$ be a set of $n \times n$ matrices. Then a non-homogeneous products of matrices drawn from S with length r is defined as $H_{s,r} = A_1 A_2 \cdots A_r$. Considering a fixed matrix in the product $H_{S,r}$ we have a homogeneous product of matrices of length r , i.e., $H_{S,r}^* = A_i A_i \cdots A_i = A_i^r$.

$$0 < Q < \frac{s_i^{(t)}}{s_j^{(t)}} < P \text{ and } 0 < Q < \frac{z_i^{(t)}}{z_j^{(t)}} < P.$$

Considering the above assumptions, [41] introduces the following transition matrix:

$$A(t) = \begin{bmatrix} f_0^{(t)} & p_0^{(t)} & 0 & \dots & \dots & 0 \\ f_1^{(t)} & 0 & p_1^{(t)} & \dots & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ f_{\beta-1}^{(t)} & 0 & 0 & \dots & \dots & p_{\beta-1}^{(t)} \\ f_{\beta}^{(t)} & 0 & 0 & \dots & \dots & 0 \end{bmatrix}.$$

He proves that in the long run the age distribution vectors $s^{(t)}$ and $z^{(t)}$ tend to be collinear or, equivalently, for each i, j ,

$$\lim_{t \rightarrow \infty} \left[\frac{s_i^{(t)}}{z_i^{(t)}} - \frac{s_j^{(t)}}{z_j^{(t)}} \right] = 0,$$

which is the rigorous statement of the weak ergodic theorem. Indeed, Lopez [41] showed that for a non-homogeneous product of the transition matrices $H_p = \prod_{t=0}^{p-1} A(t)$ and for large values of p the weak ergodicity is equivalent to a tendency for the rows of this product to differ only by a factor of proportionality, i.e., the rows tend to have the following form:

$$\begin{bmatrix} k_0 a_0^{(t)} & k_0 a_1^{(t)} & \dots & k_0 a_{\beta}^{(t)} \\ k_1 a_0^{(t)} & k_1 a_1^{(t)} & \dots & k_1 a_{\beta}^{(t)} \\ \cdot & \cdot & \cdot & \\ \cdot & \cdot & \cdot & \\ \cdot & \cdot & \cdot & \\ k_{\beta} a_0^{(t)} & k_{\beta} a_1^{(t)} & \dots & k_{\beta} a_{\beta}^{(t)} \end{bmatrix}, \quad (2.25)$$

where the $a_i^{(t)}$ change as the number t of matrices in the matrix product varies. Also, he showed that the strong ergodic theorem is a trivial corollary of the weak ergodic theorem in general.

Seneta, in his major work [57], put his effort in the study of non-homogeneous products of transition matrices that was pointed out by [41] and just discussed here. He introduced the forward and backward product of matrices as follows. First, forward products take the form:

$$H_{p,r} = \{h_{i,j}^{(p,r)}\} = A_{p+1}A_{p+2} \cdots A_{p+r}. \quad (2.26)$$

Backward products take the form:

$$U_{p,r} = \{u_{i,j}^{(p,r)}\} = A_{p+r} \cdots A_{p+2}A_{p+1}. \quad (2.27)$$

Consider a set of $(n \times n)$ matrices $\{A_{p+1}, A_{p+2}, \dots\}$ satisfying $A_k \geq 0$. Also, row- and column-allowable matrices are defined as follows.

Definition 2.5. *An $n \times n$ matrix $A \geq 0$ is row-allowable if it has at least one positive entry in each row. It is column-allowable if A^T is row-allowable. It is allowable if it is both row- and column-allowable.*

Hajnal [19] highlighted a number of useful properties of row-allowable matrices, such as the fact that a finite product of allowable matrices is also an allowable matrix. Moreover, considering an allowable $n \times n$ -matrix A and a positive n -vector $x = (x_1, x_2, \dots, x_n)^T$, then $x^T A$ and Ax are positive n -vectors. Therefore, the product of an allowable and a positive matrix is always a positive matrix. It is noteworthy that allowable matrices play a pivotal role in the study of stochastic matrices in finite Markov chains because of their interesting properties. In order to study the long run behaviour of forward products of matrices, Seneta [57] used Birkhoff's contraction coefficient (coefficient of ergodicity). He took advantage of the projective distance function, which is defined as follows:

$$d(x, y) = \ln \left(\frac{\max_i(x_i/y_i)}{\min_i(x_i/y_i)} \right) = \max_{i,j} \ln \left(\frac{x_i/y_j}{x_j/y_i} \right). \quad (2.28)$$

Also, Hajnal [19] introduced another quantity in addition to the projective distance for

a positive matrix A . It is similar to $d(x, y)$, takes values in $[0, 1]$, and is defined as follows:

$$\phi(A) = \min_{i,j,k,l} \frac{a_{ik}a_{jl}}{a_{jk}a_{il}}.$$

Note that $\phi(A) = 0$ for an allowable matrix with one or more zero entries. Then for any $x^T = (x_1, \dots, x_n) > 0$ and $y^T = (y_1, \dots, y_n) > 0$, Seneta [57] used Birkhoff's contraction coefficient (or coefficient of ergodicity) corresponding to any allowable matrix, defined as:

$$\tau_B(A) = \sup_{x,y>0, x \neq \lambda y} \frac{d(x^T A, y^T A)}{d(x^T, y^T)}. \quad (2.29)$$

This is equivalent to:

$$\tau_B(A) = \frac{1 - \sqrt{\phi(A)}}{1 + \sqrt{\phi(A)}}. \quad (2.30)$$

Since this coefficient was developed for column- allowable matrix A , $\tau_B(\cdot)$ therefore satisfies a number of fundamental and useful properties for any two column-allowable matrices A_1 and A_2 :

$$\begin{aligned} 0 < \tau_B(A_1) &\leq 1, \\ \tau_B(A_1 A_2) &\leq \tau_B(A_1) \tau_B(A_2). \end{aligned}$$

Thus, for any forward product of column-allowable matrices such as $H_{p,r}$ we have:

$$\tau_B(H_{p,r}) \leq \prod_{k=p+1}^r \tau_B(A_k).$$

Moreover, if A is of rank one as well as column-allowable, then:

$$\tau_B(A) = 0.$$

In [19], the concept of ergodicity for a sequence of products $\{H_r\}$ is defined over a sequence of matrices $\{A_f\}$ as a tendency of the sequence of products to proportionality. For a sequence of positive matrices $\{S_{p,r}\}$ of rank 1 corresponding to $\{H_{p,r}\}$, and for

fixed p , the sequence is ergodic if

$$\frac{h_{i,j}^{(p,r)}}{s_{i,j}^{(p,r)}} \xrightarrow{r \rightarrow \infty} 1 \quad \text{for all } i, j. \quad (2.31)$$

(The elements of $S_{p,r}$ are written $s_{i,j}^{(p,r)}$.)

Also, it is interesting to note that in some contexts such as in [19], the word *contractive* is used instead of ergodic. Indeed, the author believes that even though the term ergodicity is derived from the study of non-homogeneous Markov chains⁴, which has influenced the study of non-homogeneous products of matrices, there is a difference between the limiting behaviour of a Markov chain and the tendency towards rank 1 described above.

2.2.5 Ergodicity in the sense of non-homogeneous products of non-negative matrices

In the study of non-homogeneous Markov chains i.e. Markov chains in which the one-step transition probabilities are not constant, weak ergodicity is distinguished from strong ergodicity and a similar distinction is always considered for matrix products. But Hajnal [19] did not concern himself with strong ergodicity and ergodicity in the weak sense is called ergodicity for short. Relying on the introduced ergodic coefficient, Hajnal [19] stated the **ergodicity theorem** as follows:

Theorem 2.2. *Let A_1, A_2, \dots be a sequence of allowable matrices and let $H_r = A_1 A_2 \cdots A_r$ and $H_r^* = A_r A_{r-1} \cdots A_1$. Then, as $r \rightarrow \infty$, $\tau_B(H_r) \rightarrow \infty$ if and only if H_r tends to row proportionality and $\tau(H_r^*) \rightarrow 0$ if and only if H_r^* tends to column proportionality.*

Seneta [57] derived an equivalent condition for ergodicity in the weak sense as:

$$\text{for some } C > 0, \quad \frac{m_f}{M_f} > C \quad \text{for all } f, \quad (2.32)$$

⁴A discrete time Markov chain is said to be stationary or homogeneous in time if the probability of going from one state to another is independent of the time at which the step is being made. Also, Markov chain is said to be non-stationary or non-homogeneous if the condition for stationary fails.

where, m_f and M_f are, respectively, the smallest and largest elements of A_f . Hajnal, in [19, Theorem 2], showed the following slightly similar condition for **non-homogeneous matrix products**.

Theorem 2.3. *If for a sequence of allowable matrices $\{A_f\}$, $\sum_f \sqrt{\phi(A_f)} = \infty$, then a sequence of products $\{H_r\}$ defined on the sequence $\{A_f\}$ is ergodic.*

The concept of **ergodic sets** was presented in [36] in connection with the study of compact dynamical systems. The paper [19] also pointed out some interesting properties of ergodic sets by considering the following definition:

Definition 2.6. *Let $\mathcal{B}_{g,R}$ be a set of allowable matrices with the property that there is an integer g and a constant $R > 0$ such that any product H_g of length g is a positive matrix and for each $B_f \in \mathcal{B}_{g,R}$,*

$$\frac{m_f^+}{M_f^+} > R, \quad (2.33)$$

where m_f^+ and M_f^+ are the smallest and largest positive elements of B_f .

Additionally, a slight variant of the definition of an ergodic set is given as follows:

Definition 2.7. *Let $\mathcal{B}_{g,R}$ denote a set of allowable matrices with the property that there exists an integer g and a real number $R > 0$ such that if H_g is any product of length g drawn from $\mathcal{B}_{g,R}$, then*

$$\phi(H_g) > R^2. \quad (2.34)$$

Such a set will be called an ergodic set.

Hajnal [19] stated a corollary to his theorem for ergodicity of ergodic sets as follows:

Theorem 2.4. *If $\mathcal{B}_{g,R}$ is an ergodic set then a sequence of products $\{H_r\}$ drawn from $\mathcal{B}_{g,R}$ is ergodic.*

Moreover, he classified some useful properties of the sequence of products drawn from an ergodic set. Namely, eliminating matrices from such a sequence of products cannot affect ergodicity; but adding allowable matrices which are not in the set may affect ergodicity. As a result, [19] concludes that any finite set of matrices such that all products of length g are primitive is an ergodic set and consequently, a set of matrices whose incidence matrices form an ergodic set is itself ergodic if it satisfies (2.34) or (2.33). Likewise, Hajnal [19] provides a short list of examples of ergodic sets in empirical cases as follows:

- Any primitive incidence matrix.
- Any set of primitive incidence matrices which commute.
- The special incidence matrices used in the weak ergodic theorem of demography (Coale-Lopez theorem [41]). Ones occur in certain positions in the top row of each matrix and in the first sub-diagonal.
- The set \mathcal{G} of primitive incidence matrices such that if $\tilde{G} \in \mathcal{G}$ and \tilde{F} is primitive then $\tilde{G}\tilde{F}$ and $\tilde{F}\tilde{G}$ are primitive. This set is studied in a number of papers in the context of non-homogeneous Markov chains by Sarymsakov and collaborators [55].

In addition, every primitive Leslie matrix is by itself an ergodic set [19]. Earlier, we saw that one of the conditions of the definition of ergodic set is having a strictly positive matrix as a product of any g members of ergodic set, where g is some fixed positive integer. Note that in biology and demography, there are several types of reducible matrices M_q such that the product $H(1, q)$ may not be a positive matrix, but a non-negative matrix, and these obviously do not satisfy the conditions introduced in [19] for an ergodic set. Thus, in his fundamental work, Cohen [8] tried to adjust the conditions to some cases of biological interest. For instance, he showed that each primitive Leslie matrix is itself an ergodic set only by itself; we will review this work later. In fact, Cohen started with $n \times n$ non-negative non-zero matrices M which may be written in

normal and canonical form:

$$M = \begin{bmatrix} A & 0 \\ B & C \end{bmatrix}, \quad (2.35)$$

where A is an irreducible $n_1 \times n_1$ matrix, C is a $n_2 \times n_2$ matrix and $n = n_1 + n_2$. Using this form, Cohen developed a strong ergodic theorem to show that in order to have ergodic *exponentially contracting sets*, we only need to confine our attention to matrices with a certain pattern of positive and zero elements as the members of the set. For instance, subject to some quantitative restrictions on the elements of the matrices, any set consisting of matrices with each of the following patterns of positive elements can be exponentially contracting sets:

$$M_1 = \begin{bmatrix} + & 0 & 0 \\ + & + & 0 \\ 0 & + & 0 \end{bmatrix} \quad M_2 = \begin{bmatrix} + & 0 & 0 \\ + & + & 0 \\ 0 & + & + \end{bmatrix} \quad M_3 = \begin{bmatrix} + & + & 0 \\ 0 & + & 0 \\ 0 & + & + \end{bmatrix} \quad (2.36)$$

$$M_4 = \begin{bmatrix} + & 0 & 0 \\ + & 0 & 0 \\ 0 & + & 0 \end{bmatrix} \quad M_5 = \begin{bmatrix} + & + & 0 \\ + & 0 & 0 \\ 0 & + & 0 \end{bmatrix} \quad M_6 = \begin{bmatrix} 0 & + & + \\ + & 0 & 0 \\ 0 & + & 0 \end{bmatrix}.$$

The ‘+’ signs indicate positive numbers. Practically, each positive element $m_{i,j}$ indicates a transition from a category j to a category i . Products of a sufficiently large number of matrices of the form M_i are column-positive but not positive for any single $i = 1, 2, \dots, 5$ while the products of a sufficiently large number of matrices like M_6 , are positive. For the first five types of matrices, their irreducible sub-matrices in form (2.35) are of orders 1, 1, 1, 2 and 3, respectively. The patterns introduced in [8] are compatible forms of matrices arising in biological and demographical cases. Namely, M_1 is a linear formalization of a compartmental model for the ontogeny of blood forming cells [3], M_2 is a model of a 3-stage educational system in which individuals either remain in their present state or are promoted at the end of each time period [58], M_3

models the course from one (discrete) generation to the next of the proportions of individuals of genotypes AA, Aa and m, allowing for differential fertility, viability and geometric selection. Finally, M_4 , M_5 and M_6 are all special cases of the demographic projection matrix for a closed, single-sex population with 3 age groups (young, middle, old). The elements of the first row describe age-specific fertility, those of the sub-diagonal age-specific survival.

2.2.6 Ergodicity in the sense of Markov chains

The advantages of the approach in [8] as compared with the weak ergodic theorem of Lopez becomes apparent when in the Lopez model, for certain choices of y_0 and X (the set of possible operators x_n), y_n approaches a possibly time-variant sequence dependent on the sequence $\{x_n\}$ and not on y_0 . This is carefully addressed in Cohen's work. Stating the theorems of Cohen's work requires introducing a new literature of studies of Markov chains. Therefore, here we just stick to explain the result of each theorem.

In a first theorem, Cohen [8] showed how the joint process (x_n, y_n) of operators and points (vital rates and age structures) could be written explicitly in terms of the transition function governing $\{x_n\}$. In a second theorem, [8] showed that by assuming ergodic conditions on the homogeneous chain X and using the equivalent ergodic theorem of demography, then the behaviour of the joint chain $\{(x_n, y_n)\}$ also has an ergodic feature. A third theorem in Cohen's paper reveals that if we consider the same condition as in his second theorem with a non-homogeneous chain X , then the joint chain converges in distribution to an invariant long run distribution. Finally, a fourth theorem in [8] emphasized that even under stronger conditions on the smoothness of the operators from X , the bivariate chain $\{(x_n, y_n)\}$ satisfies the stronger ergodic condition if $\{x_n\}$ is homogeneous and the rate of convergence is exponential. Additionally, there are a number of interesting results associated with his main theorems. For instance, a model for estimating the transition function of the chain on X based on the historical data of vital rates is suggested. A simple direct technique for obtaining the exact mean and an

approximate variance of the number of individuals of each age is provided by the third Cohen work [9]. Doing so, the exact mean and an approximate variance of the total population size could be calculated and consequently the so-called exact population long-run growth rate.

Tuljapurkar and Orzack [63] studied the mean logarithmic growth rate and a logarithmic variance as important components of population growth which significantly describe the growth of a population in the long run. They considered an age-structured population influenced by different sets of environmental conditions at different times. They showed that the distribution of the total population is log-normal when it is assumed that the Leslie matrix in each time interval is chosen by a Markov process. In fact, [63] considers a more realistic population model with varying vital rates (fecundity and mortality). Also, the authors defined the different environmental states in terms of a set of variables such as temperature, rainfall and humidity. The biological assumptions in their work are based on the assumptions in [19, 57] that guarantees weak ergodicity. These conditions consist of irreducibility, primitivity of Leslie matrices, as well as having the same pattern of non-zero elements for all Leslie matrices in the same sequences (i.e., sharing the same incidence matrix). The latter condition is equivalent to having a fixed group of reproductive ages (or stages) in different environmental conditions and to assuming that there should be always a non-zero probability of surviving to the same final stage in all environments. The authors started their study with the Leslie model as follows:

$$\bar{N}_{t+1} = X_{t+1}\bar{N}_t = X_{t+1}X_t \dots X_0\bar{N}_0, \quad (2.37)$$

where \bar{N}_t is a column vector with the distribution of numbers of individuals in successive age classes at time t . It is assumed that the values of the random matrices X_t are chosen from a set of $n \times n$ matrices. If M is any matrix in this set, its elements m_{ij} satisfy

$$\min^+(m_{ij}) > \beta > 0, \quad \max(m_{ij}) < \gamma < \infty. \quad (2.38)$$

The above mentioned assumption is named **A1**. Assumption **A2** is on the possible values for X_t , which should be selected from an ergodic set; i.e., there is positive integer g such that the product of any g matrices M_1, M_2, \dots, M_g is a matrix with strictly positive elements,

$$(M_1 M_2 \dots M_g)_{ij} > 0, \quad \text{for all } i, j. \quad (2.39)$$

A3 indicates the assumption on the sequence X_1, X_2, X_3, \dots such that it forms a Markov chain with a homogeneous transition probability function $P(a)$:

$$P_n(x, A) = P\{X_{m+n} \in A | X_m = x\} \quad (2.40)$$

for the n -step transition probability function of the Markov chain, where x is drawn from A (a measurable set belonging to the range of X_t) and there exists a unique stationary probability distribution $\Pi(A) = P\{X_t \in A\}$. The described X -process has only one ergodic set and this set contains no cyclically moving subsets. Also,

$$|P_n(x, A) - \Pi(A)| \leq D_2 \rho_2^n, \quad (2.41)$$

where $0 \leq D_2 < \infty, 0 \leq \rho_2 < 1$ are positive constants and n a positive integer.

2.2.7 Asymptotic analysis in the presence of variable vital rates

Having predictable or unpredictable temporal variation in different Leslie matrices X_t motivated a variety of studies. Namely, Lopez's result, the weak ergodic theorem of demography, is one of the primary works in the case of predictable, deterministic patterns of temporal variation in population vital rates. In the presence of an unpredictable pattern of temporal variation, [50] and particularly [60] carried out a derivation of the mean and variance for the population vector using some recursion equations.

Tuljapurkar and Orzack's work [63] focuses on the distribution of the population growth rate in the case of unpredictable temporal variation in vital rates. They consider

the successive Leslie matrices in (2.37) to be a random sequence which is determined by a Markov process defined on environmental states. Each possible random sequence of matrices in (2.37) is labelled by an index ω , an initial population vector \bar{N}_0 and a total population \bar{M}_0 . They consider $M_t = \|\bar{N}_t\|$, the total population number at time t , where the norm is defined as follows:

$$\|B\| = \sum_i |B_i|, \quad i = 1, \dots, n.$$

The *cumulative growth* in total population number at time t and environmental sequence ω is defined as

$$\Lambda_t(\omega) = \frac{M_t(\omega)}{M_0}. \quad (2.42)$$

In order to describe environmental variation, [16] assumes s distinct environmental states with corresponding matrices $\mathbf{M}_1, \mathbf{M}_2, \dots, \mathbf{M}_s$. The Markov chain which manages the transition between the matrices of vital rates is described by an $s \times s$ matrix \mathbf{P} of transition probabilities with elements $p_{ij} = P\{\mathbf{X}_{t+1} = \mathbf{M}_j | \mathbf{X}_t = \mathbf{M}_i\}$. It is assumed that there is a stationary probability distribution defined as a row vector $\tilde{\mathbf{\Pi}}' = (\mathbf{\Pi}_1, \dots, \mathbf{\Pi}_s)$ where $\mathbf{\Pi}_i = P\{\mathbf{X}_t = \mathbf{M}_i\}$ for $i = 1, \dots, s$ and $\tilde{\mathbf{\Pi}}' \mathbf{P} = \tilde{\mathbf{\Pi}}'$.

Population growth rate characteristics in the long run

The authors in [63] consider four indices that characterize population growth in the long term. They introduce λ^* as the geometric rate of growth of the population, where $\lambda^* = \lim_{t \rightarrow \infty} (\ln E[\Lambda_t]/t)$ and $E[\Lambda_t]$ is the expectation of Λ_t . The second quantity introduced in [63] is the mean geometric growth rate $\exp(a)$, where $a = \lim_{t \rightarrow \infty} (\ln E[\ln \Lambda_t]/t)$. The next quantity is the scaled variance $\sigma^2 = \lim_{t \rightarrow \infty} (\ln E[\Lambda_t]/t)$. Finally, modal populations grow at a geometric rate λ_m with $\lambda_m = \lim_{t \rightarrow \infty} ([\ln \Lambda^*]/t)$.

Additionally, [9] points out two natural measures of the long-run rate of growth per unit time of a similar Markovian chain system: the average of the growth rates of the individual sample paths λ and the growth rate of the average of the sample paths μ .

Mean logarithmic growth rate boundaries

The authors in [63] proved that

$$\log \lambda = \lim_{t \rightarrow \infty} t^{-1} E [\log Y_i(n)], \quad (2.43)$$

where the Y_i are random non-negative s -vectors satisfying the geometric model of population growth.

Cohen in [9] offered an important upper and lower bound for $\log \lambda$ as follows:

$$-\infty < \sum_{i=1}^s \Pi_i \log c_i < \log \lambda < \sum_{i=1}^s \Pi_i \log \|\mathbf{M}_i\| < \infty, \quad (2.44)$$

where c_i is the smallest column sum of the matrix \mathbf{M}_i , and $\|\mathbf{M}_i\| = \sup_{\|y\|=1} \{\|\mathbf{M}_i y\|\}$ which is the largest column sum of M_i . Consequently, for the mean logarithmic growth rate a introduced above, we have:

$$\sum_{i=1}^s \Pi_i \ln c_i < a < \sum_{i=1}^s \Pi_i \ln C_i, \quad (2.45)$$

where c_i is the smallest column sum of the matrix \mathbf{M}_i and C_i is the largest column sum of \mathbf{M}_i . Also, in [63] the authors show that, for every \mathbf{M}_i one has $0 < \lambda_i \leq C_i$, so that $C_i < 1$ implies $\lambda_i < 1$, which is equivalent to a bad environmental condition; and conversely a good environmental condition can be characterised by $C_i > 1$.

Cumulative growth of the total population

Based on the geometric growth model (2.37), the authors in [63] conclude that the natural analog of the ultimate rate of increase is $t^{-1} \ln[\frac{M_t}{M_0}] = t^{-1} \ln \Lambda_t$. They assume that the serial autocorrelation of the environment decays fairly rapidly, that there is a long-run stable frequency distribution of different environments and that each possible sequence of matrices in (2.37) is weakly ergodic in the demographic sense. They show that the logarithm of the cumulative growth is asymptotically normally distributed for

large times as follows:

$$\ln \Lambda_t \rightarrow \sim N(at, \sigma^2 t), \quad (2.46)$$

where $t \rightarrow \infty$ and a, σ^2 are the scaled mean and variance of normal distribution. In fact, they use a special case of the theorem for non-negative matrices in [14] and a Markov process that is ergodic but not necessarily stationary. As a result, they show that Λ_t has a log-normal asymptotic distribution. Then the vector of proportions in different age classes is defined as

$$\bar{Z}_i = [\bar{N}_i/M_i], \quad \sum_{i=1}^n \bar{Z}_i = 1$$

Using the introduced vectors, (2.37) can be written as coupled equations in terms of the dynamics of $\bar{N}_t(\omega)$ as follows:

$$\bar{Z}_{t+1} = \frac{X_{t+1}\bar{Z}_t}{\|X_{t+1}\bar{Z}_t\|} = \frac{{}^{t+1}Y^1\bar{Z}_0}{\|{}^tY^1\bar{Z}_0\|}, \quad (2.47)$$

$$M_{t+1}(\omega) = \|X_{t+1}\bar{Z}_t\|M_t = \|{}^{t+1}Y^1\bar{Z}_0\|. \quad (2.48)$$

Here M_0 and \bar{Z}_0 are fixed initial quantities, and the notation

$${}^{k+m}Y^m = X_{k+m}X_{k+m-1} \dots X_m,$$

is used. Therefore, the cumulative growth of the total population can be written using only the matrix product ${}^tY^1$. Focusing on the random matrix products ${}^tY^1$, [63] provided their main argument using three steps as follows:

- **Step 1:** Based on **A1** and **A2**, the matrix product ${}^tY^1$ is definable such that for large t , it has totally positive elements that are not of huge difference in magnitude. Thus, $\ln \Lambda_t$ depends significantly on $\|{}^tY^1\|$.
- **Step 2:** Assumptions **A1** and **A2** guarantee demographic weak ergodicity (i.e., a tendency of ${}^tY^1$ to proportionality). Consequently, ergodicity assures the existence of a limiting distribution of \bar{Z}_t .

- **Step 3:** The successive growth rates are $[\Lambda_{t+1}/\Lambda_t]$, which in the long run become asymptotically independent of past growth rates.

Mean logarithmic growth rate evaluation

Based on previously discussed concepts, [63] proved the relation (2.44) in the following theorem:

Theorem 2.5. *Assume A1, A2 and A3. Then a , the mean logarithmic growth rate, is given by*

$$a = E_F \left[\ln \frac{(X_{k+2}\bar{Z}_{k+1})_1}{(\bar{Z}_{k+1})_1} \right], \quad (2.49)$$

where $E_F[p]$ is the expectation of p with respect to the stationary measure on the bivariate chain (X_t, \bar{Z}_t) determined by the stationary distribution $F(\cdot, \cdot)$. The scaled logarithmic variance σ^2 is given by

$$\sigma^2 = C_1 + 2 \sum_{r=2}^{\infty} C_r, \quad (2.50)$$

where C_i is the largest column sum of growth matrices M_i correspond to environment state i . Also,

$$\lim_{t \rightarrow \infty} P \left\{ \frac{\ln \Lambda_t - at}{\sigma t^{1/2}} \leq z \right\} = \frac{1}{(2\pi)^{1/2}} \int_{-\infty}^{\infty} e^{-u^2/2} du, \quad (2.51)$$

if $\sigma^2 \neq 0$. If $\sigma^2 = 0$ then with probability one as $t \rightarrow \infty$,

$$\frac{\ln \Lambda_t - at}{\sigma t^{1/2}} \rightarrow 0. \quad (2.52)$$

The authors of [63] concentrate on the rate of convergence of $\ln \Lambda_t$ to a normal distribution using numerical simulation of (2.37) where a particular Markov process governs the Leslie matrices of the model. Utilizing a number of analytical and numerical methods, the authors realize that not only is the scaled logarithmic mean a com-

pletely insensitive to environmental autocorrelation, but it is also determined by the joint effect of the magnitude of variation between vital rates in different environments. Conversely, the variance σ^2 is highly sensitive to environmental autocorrelation.

New measurements for long run growth rate of the total population: $\lambda(\bar{\mathbf{M}})$, λ_G

In addition to the four introduced quantities for the long run growth rate of a population, [63] suggests two approximations of the long run growth rate of the total size of the population. The first approximation is introduced as the largest eigenvalue $\lambda(\bar{\mathbf{M}})$ of the average matrix $\bar{\mathbf{M}} = \sum_i \Pi_i \mathbf{M}_i$. When comparing with other quantities for population growth, [10] showed that $\lambda(\bar{\mathbf{M}}) \neq \lambda^*$. Tuljapurkar and Orzack [63] showed that $\lambda(\bar{\mathbf{M}}) \neq \lambda_m$ and $\lambda(\bar{\mathbf{M}}) \neq \exp(a)$. The geometric mean of dominant eigenvalues λ_G is introduced as the second approximation of population growth rate, which is defined as follows:

$$\ln \lambda_G = \sum_i \Pi_i \ln \lambda_i. \quad (2.53)$$

In fact, λ_G is more capable to demonstrate the long run growth rate than $\lambda(\bar{\mathbf{M}})$, since it is proved by Marcus and Minc [45] that λ_G has the same bounds as $\exp(a)$. In other words, since $c_i < \lambda_i < C_i$, then

$$\sum_i \Pi_i \ln c_i < \ln \lambda_G < \sum_i \Pi_i \ln C_i. \quad (2.54)$$

Sensitivity of the growth rate

The sensitivity of the growth rate to three important influential factors in random environments is also discussed in [63]:

- (i) Sensitivity to variation among elements of the matrices $\mathbf{M}_i, i = 1, \dots, s$, measured by:

- (a) $\Delta_{jk} = \max_{i,i'} \{(\mathbf{M}_i)_{jk} - (\mathbf{M}_{i'})_{jk}\}$, where $i, i' = 1, \dots, s$ and $k = 1, \dots, n$
 - or,

(b) in terms of the element-wise variance of the random matrix X_t with respect to the equilibrium distribution $\bar{\Pi}$.

(ii) Sensitivity to the equilibrium probability $\bar{\Pi}$.

(iii) Sensitivity to the rate at which the environmental process “forgets” the past.

Based on these factors, [63] shows that a is likely to be insensitive to autocorrelation, while σ^2 should be very sensitive to autocorrelation. Also, σ^2 depends quadratically on variation among matrices. However, two general scenarios of a population in a fluctuating environment are pointed out:

- an environmental pattern consisting of a set of environmental states and a rule for their temporal sequencing,
- a life history specifying the population vital rates corresponding to each environmental state.

The paper [63] claims that the comparison of life histories could be scaled to comparing factors of population growth, and equivalently fitness could be defined. After reviewing some biological evidence, they conclude that the triple $(a, \sigma^2, Q_0(t))$ could be used as a proper descriptor of fitness in terms of growth, distribution and extinction of the total population (i.e. $Q_0(t) = P\{M_t = 0\}$). Finally, a species with smaller growth rate a could result in a higher fitness because of smaller $Q(t)$ and decreasing σ^2 .

Effects of environmental variation on the rate of extinction

Tuljapurkar and Orzack [63] explore the effect of environmental variation on the rate of extinction, including both analytic and numerically simulated results. Instead of having zero population for the definition of extinction, any M_t less than unity corresponds to an extinction situation. Thus, $M_t = 1$ is introduced as the extinction boundary and [63] define the extinction probability at time $i = t$ as follows:

$$Q_1(t) = P\{M_s(\omega) < 1, s \leq t\}. \quad (2.55)$$

They show that in the long-run, $Q(t) = F(-\frac{\ln M_0}{\sigma t^{1/2}} - \frac{at^{1/2}}{\sigma})$, where $F(z)$ is the area under the standard normal curve in the interval $(-\infty, z)$. As a result, when $t \rightarrow \infty$ and $a < 0$, $Q(t) \rightarrow 1$. Thus, for $a = 0$, $Q(t) \rightarrow 1/2$, while for $a = 1$, $Q(t) \rightarrow 0$. The aforementioned results for the limiting extinction probabilities as $t \rightarrow \infty$ are summarized as follows:

$$Q_1(\infty) = 1, \text{ if } a \leq 0, \tag{2.56a}$$

$$0 < Q_1(\infty) \leq 1, \text{ if } a > 0. \tag{2.56b}$$

Equivalent to the conditions for a , namely $a > 0$, $a = 0$ and $a < 0$ the authors [63] suggested supercritical, critical and sub-critical cases, respectively. In the supercritical case, it is stated that $\exp(-a \ln M_0 / \sigma^2)$ is a proper lower bound for $Q_1(\infty)$. Finally, [63] points out some interesting work in which the reviewed model is used to study the dynamics of size structured populations with non-Markov sequences of vital rates but with some restrictions.

Chapter 3

Dynamics of Arctic Charr population in a constant environment

In this chapter, assuming a constant environment and using a discrete time framework, a matrix model is formulated to describe the behaviour of the Arctic Charr population. We form the model to account for both age- and stage structure of the population. Then we study the long term behaviour of the population. In order to estimate the parameters of the model, we formulate the parameter estimation problem with a generalized weighted least square method, then we estimate the parameter of model utilizing a genetic algorithm based on a database consisting of 39 years of historical data on the Arctic Charr population in Cambridge Bay. Finally, we discuss the sensitivity growth rate to the parameter of the model.

3.1 Methodology

3.1.1 Biological model

The life-cycle of Arctic Charr is summarized using six stages consisting of juveniles, immature, mature, reproducing, post-reproduction and old. More specifically:

- **Juvenile stage:** Individuals five years and younger are in the juvenile stage. First-time migration to sea water is highly dependent on the size of individuals; migrant individuals need to be at least 11–20 cm in length to handle the change

from fresh to sea water [29]. It is assumed that migration does not occur during the juvenile stage of the Anadromous Arctic Charr life-cycle.

- **Immature stage:** Individuals that undertake migration to sea are considered immature (before they are mature enough to reproduce). The duration of residence in this stage varies between 3 and 14 years; thus individuals in this stage are aged from 5 to 18 years. Individuals who stay the whole 14 years in the immature stage skip the mature stage and eventually become old [29].
- **Mature stage:** The age of maturity is highly dependent on the individual's body development indices (weight and length) [29]. Hence, after spending enough time in the immature stage, a proportion of immature individuals having a sufficiently good body condition become mature; in the mathematical model (3.1.2) we denote this proportion by α . The maximum duration of stay in the mature stage is assumed to be 12 years for anadromous Arctic Charr. During this stage, Charrs undertake migrations to sea, usually from mid-to-late June until mid-August to early-September [29]. High access to rich food resources during summer migration induces a high growth rate for Arctic Charr and accelerates their maturity and, as a result, increases their ability to reproduce.
- **Reproducing stage:** Each year, a proportion of mature individuals become reproducers (in (3.1.2), we denote this proportion by β). The Arctic Charr's ability to reproduce is extremely dependent on their body development [29]. However, it is assumed that individuals between 9 and 20 years are able to join the reproducing stage. Also, we assumed each independent of the age and body condition an individual produces the same number of eggs (which is denoted f in (3.1.2)).
- **Post-reproduction stage:** Since the reproduction process costs about 30% of the reproducer's body mass, the reproducers skip at least one year reproduction [29]; in this thesis this obligatory gap is called the post-reproduction stage. These individuals undertake migrations to sea. It is assumed that all individuals stay in the post-reproduction stage a single year. Thus, this stage can be visited between

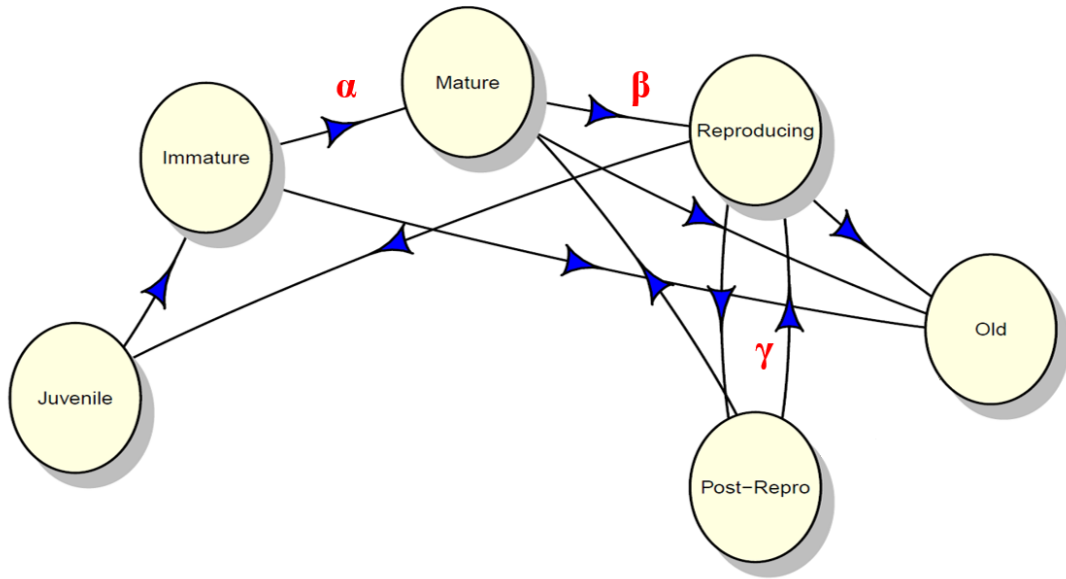


Figure 3.1: Arctic Charr life cycle digraph based on stage structure of the population.

the ages of 10 and 18 years. After the post-reproduction stage, individuals that are not too old can return to the mature stage (the proportion of such individuals is denoted γ in (3.1.2)).

- **Old Stage:** In each stage (except for the juvenile stage) there is a possibility for individuals of age 18 and older to enter to the old stage and stay there for the remainder of their life; i.e., individuals in the old stage cannot reproduce any more.

Of course, individuals of all ages and stages may also die, so there are survival probabilities for juveniles, immature, mature, reproducing, post-reproducing and old stage. These survivals are denoted respectively by S_J , S_I , S_M , S_R , S_P and, S_O .

The whole life-cycle is shown in Figure 3.1.

3.1.2 Mathematical model

Given the life-cycle of the Arctic Charr population, we form a stage- and age-structured model. Since the available data on Arctic Charr population is collected annually, a discrete-time model is used, with a time step of one year. In each stage, the age of individuals is indicated as the index; therefore, $X_i(t)$ represents the number of females

of age i in stage X on year t . Having both age and stage structure requires allocating different survival rates for individuals in the same stage but in different age classes.

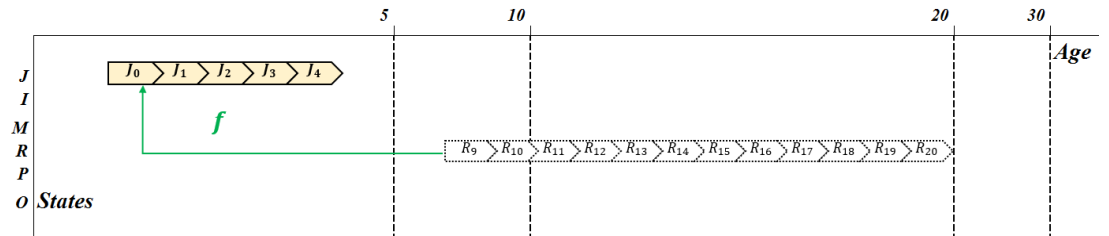
The four types of parameters in the model are:

- Survival rates S_{X_i} indicate the proportion of the population in stage X and of age i at time t that survives to age $i + 1$ at time $t + 1$, where $i \in \{1, 2, \dots, 31\}$. Note that the oldest observed individual in available database (utilised in the current study) has 31 years.
- The fecundity of reproducing individuals, denoted f , is assumed to be equal for all reproducing individuals regardless of their age.
- The rate of transition from the immature to the mature stage is denoted α .
- The rate of transition from mature to reproducing individual is denoted β .
- The rate of transition from post-reproduction to reproducing individual is denoted γ .

Based on parameters and given assumptions, a mathematical model is established. We formulate the model by focusing on the age of individuals. In each part of the model, first a schematic illustration of transitions is presented and then the related mathematical model is shown. Neighbouring compartments separated by solid lines indicate allowed progress into the same stage from age i to age $i + 1$, e.g., I_{11} to I_{12} in following graphs; compartments separated with black dotted lines indicate transitions which cannot happen; e.g., post-reproducing individuals of age i can not stay in post-reproducing stage in the next year when they are $i + 1$ years old, i.e. transitions from P_i to P_{i+1} is impossible. Same for reproducers, individuals in this stage of age i can not reproduce again in the next year, so transition from R_i to R_{i+1} is impossible (it is assumed individuals stay in post-reproducing stage only for one year and do not reproduce in two consecutive years). Green arrow links reproducers to juveniles of age 0 (J_0). Blue dotted arrows show transitions from post-reproducing to reproducing stages/ages. Red dotted arrows show transitions from the post-reproducing stage to the mature stage.

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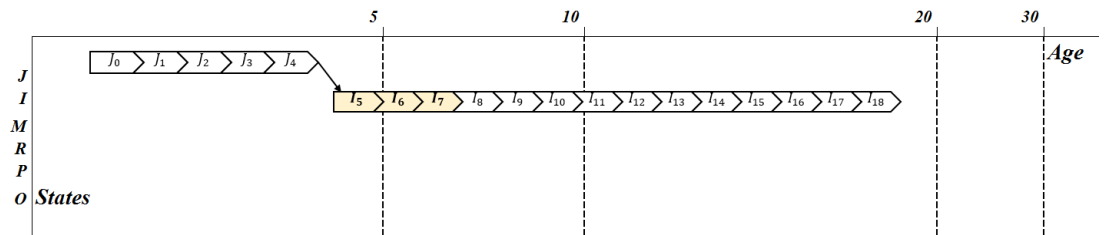
- **Age 0–4 years:** The transitions of 0 to 4 years old individuals members of the juvenile stage.



$$J_0(t+1) = \sum_{k=9}^{20} fR_k(t) \quad (3.1.a)$$

$$J_i(t+1) = s_{J_{i-1}}J_{i-1}(t), \quad i = 1, \dots, 4. \quad (3.1.b)$$

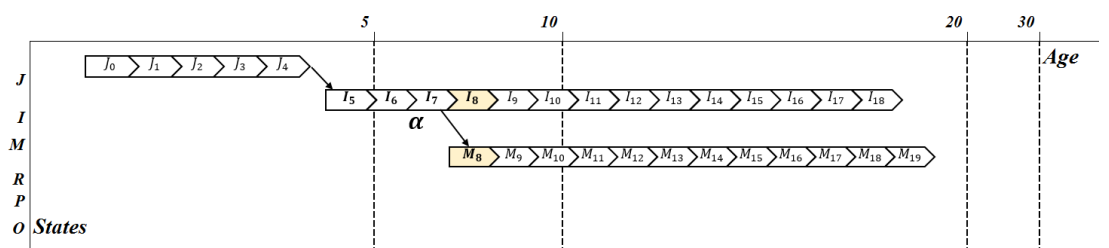
- **Age 5–7 years:** 6 and 7 years old individuals belong to the immature life stage.



$$I_5(t+1) = s_{J_4}J_4(t) \quad (3.1.c)$$

$$I_i(t+1) = s_{I_{i-1}}I_{i-1}(t), \quad i = 6, 7. \quad (3.1.d)$$

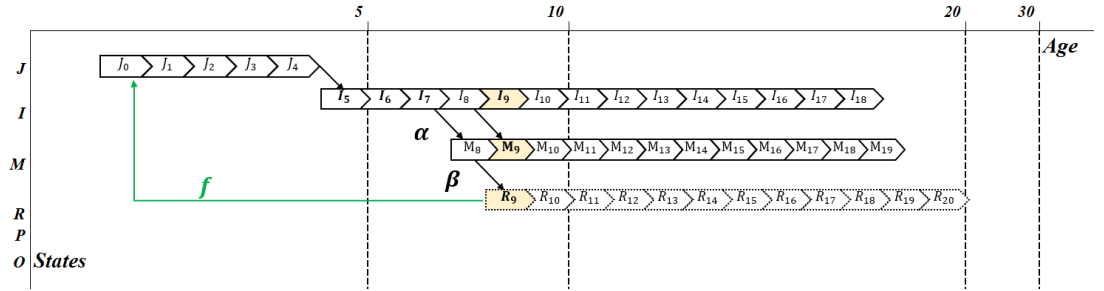
- **Age 8 years:** Individuals that are of age 8 years can be either immature or have progressed to the mature stage.



$$I_8(t + 1) = (1 - \alpha)s_{I_7}I_7(t) \quad (3.1.e)$$

$$M_8(t + 1) = \alpha s_{I_7}I_7(t). \quad (3.1.f)$$

- **Age 9 years:** In favourable circumstances, immature individuals of age 8 progress to the mature stage in the next year; some are even able to reproduce (when they turn 9 years old).



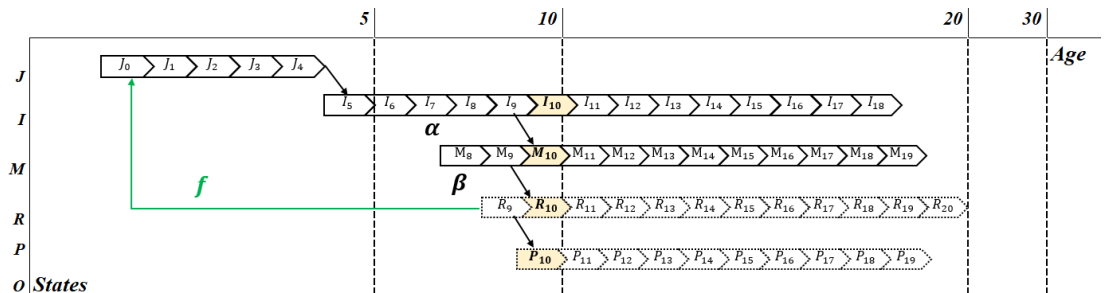
Thus, 9 years old individuals can be immature, mature or reproducing, with transitions governed by the following equations:

$$I_9(t + 1) = (1 - \alpha)s_{I_8}I_8(t) \quad (3.1.g)$$

$$M_9(t + 1) = \alpha s_{I_8}I_8(t) + (1 - \beta)s_{M_8}M_8(t) \quad (3.1.h)$$

$$R_9(t + 1) = \beta s_{M_8}M_8(t). \quad (3.1.i)$$

- **Age 10 years:** A 9 years old Arctic Charr that reproduced in year t skips reproducing and spends one year in the post-reproductive stage. Hence, 10 years old individuals can be in immature, mature, reproducing or post-reproduction stages.



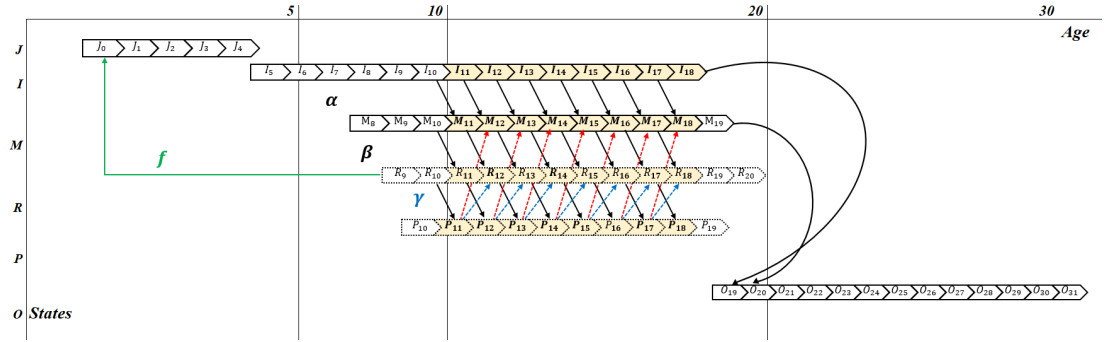
$$I_{10}(t + 1) = (1 - \alpha)s_{I_9}I_9(t) \quad (3.1.j)$$

$$M_{10}(t + 1) = \alpha s_{I_9}I_9(t) + (1 - \beta)s_{M_9}M_9(t) \quad (3.1.k)$$

$$R_{10}(t + 1) = \beta s_{M_9}M_9(t) \quad (3.1.l)$$

$$P_{10}(t + 1) = s_{R_9}R_9(t). \quad (3.1.m)$$

- **Age 11–18 years:** Individuals of age $i = 11, \dots, 18$ can be any of the aforementioned stages. Some transitions from the post-reproducing to the reproducing stage exist, corresponding to individuals who get ready to reproduce again after one year of being in the post-reproducing stage.



$$I_i(t + 1) = (1 - \alpha)s_{I_{i-1}}I_{i-1}(t) \quad (3.1.n)$$

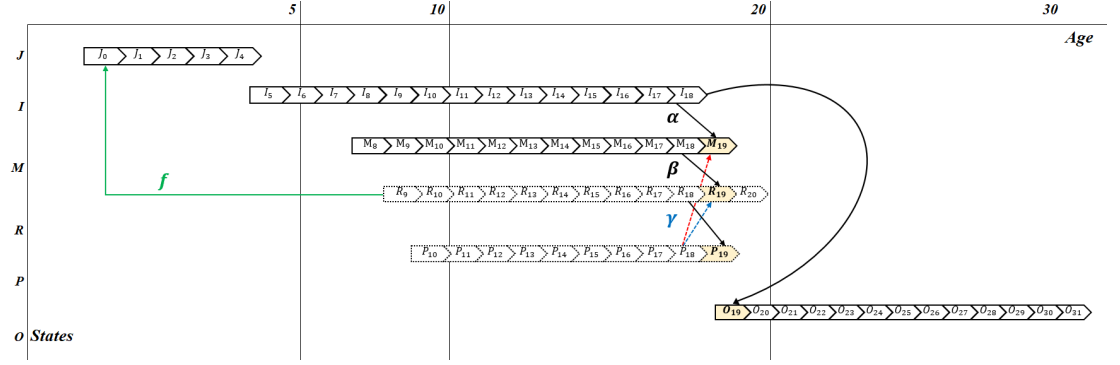
$$M_i(t + 1) = \alpha s_{I_{i-1}}I_{i-1}(t) + (1 - \beta)s_{M_{i-1}}M_{i-1}(t) + (i - \gamma)s_{P_{i-1}}P_{i-1}(t) \quad (3.1.o)$$

$$R_i(t + 1) = \beta s_{M_{i-1}}M_{i-1}(t) + \gamma s_{P_{i-1}}P_{i-1}(t) \quad (3.1.p)$$

$$P_i(t + 1) = s_{R_{i-1}}R_{i-1}(t). \quad (3.1.q)$$

- **Age 19 years:** The following equations represent the dynamics of fish when they are 19 years old:

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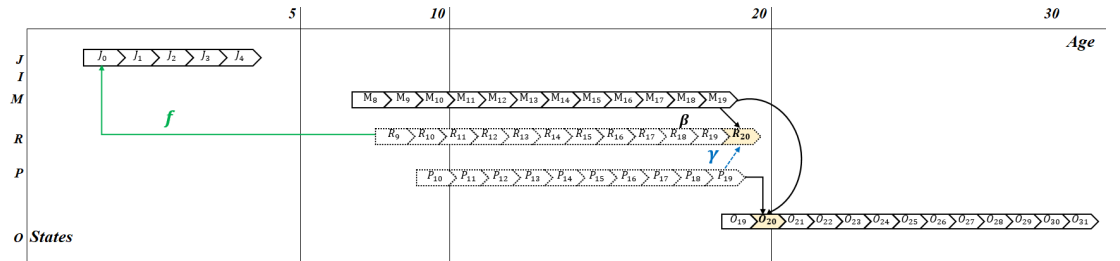
$$M_{19}(t + 1) = \alpha s_{I_{18}} I_{18}(t) + (1 - \beta) s_{M_{18}} M_{18}(t) + (1 - \gamma) s_{P_{18}} P_{18}(t) \quad (3.1.r)$$

$$R_{19}(t + 1) = \beta s_{M_{18}} M_{18}(t) + \gamma s_{P_{18}} P_{18}(t) \quad (3.1.s)$$

$$O_{19}(t + 1) = (1 - \alpha) s_{I_{18}} I_{18}(t) + s_{R_{18}} R_{18}(t) \quad (3.1.t)$$

$$P_{19} = s_{R_{18}} R_{18}(t) \quad (3.1.u)$$

- **Age 20 years:** Reproducing and old individuals aged 20 are described by the following equations:



$$R_{20}(t + 1) = \beta s_{M_{19}} M_{19}(t) + \gamma s_{P_{19}} P_{19}(t) \quad (3.1.v)$$

$$O_{20}(t + 1) = s_{O_{19}} O_{19}(t) + s_{R_{19}} R_{19}(t) + (1 - \beta) s_{M_{19}} M_{19}(t) + (1 - \gamma) s_{P_{19}} P_{19}(t). \quad (3.1.w)$$

- **Age 21 years:** 20 years old individuals are the last who can reproduce, so the number of old individuals of age 21 is given by:

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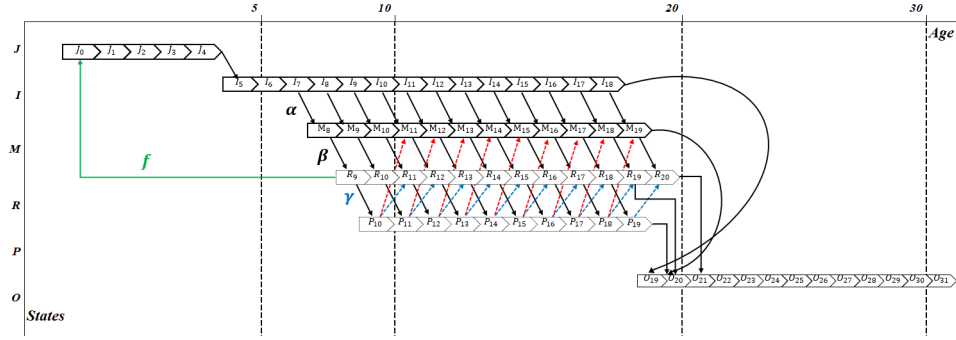
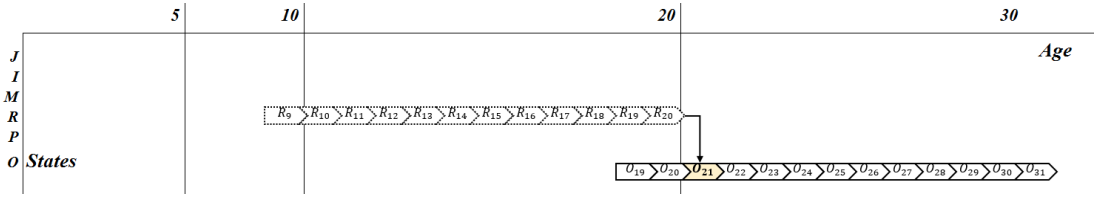
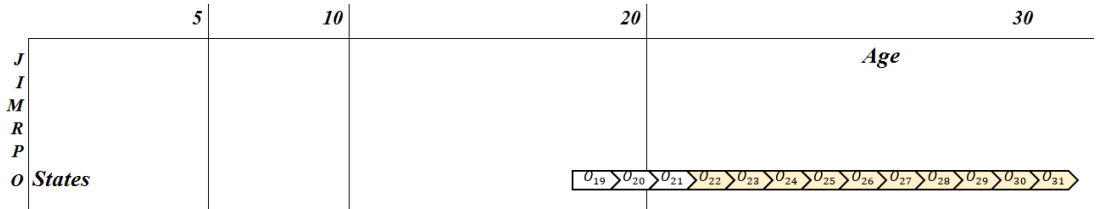


Figure 3.2: Full age and stage structure of the Arctic Charr life-cycle model.



$$O_{21}(t+1) = s_{O_{20}}O_{20}(t) + s_{R_{20}}R_{20}(t). \quad (3.1.x)$$

- **Age 22 years and older:** Finally, transitions corresponding to individuals older than 22 years take the following form:



$$O_i(t+1) = s_{O_{i-1}}O_{i-1}(t), \quad i = 22, \dots, 31. \quad (3.1.y)$$

To sum up, the mathematical model has 68 parameters (64 survival rates S_{X_i} , α , β , γ and f) and 64 compartments. In Figure 3.2, all transitions are shown.

A matrix representation $\mathbf{\Pi}$ of the model is given by (3.2), in which the notation $[A \rightarrow B]$ indicates a block with transitions from age a in stage A to age $a + 1$ in stage B . Note that 0's represent blocks of zeros of the appropriate size.

$$\mathbf{\Pi} = \begin{pmatrix} [J \rightarrow J] & 0 & 0 & [R \rightarrow J] & 0 & 0 \\ [J \rightarrow I] & [I \rightarrow I] & 0 & 0 & 0 & 0 \\ 0 & [I \rightarrow M] & [M \rightarrow M] & 0 & [P \rightarrow M] & 0 \\ 0 & 0 & [M \rightarrow R] & 0 & [P \rightarrow R] & 0 \\ 0 & 0 & 0 & [R \rightarrow P] & [R \rightarrow P] & 0 \\ 0 & [I \rightarrow O] & [M \rightarrow O] & [R \rightarrow O] & 0 & [O \rightarrow O] \end{pmatrix} \quad (3.2)$$

The age structure implies that diagonal entries are zero, as in Leslie matrices, since individuals cannot stay in the same age after one transition. The stage structure and loops between the mature, reproducing and post-reproductive stages yields a block matrix that resembles Lefkovitch matrix. The columns show the position of individuals at time t , rows represent their position at time $(t + 1)$. The transition matrix $\mathbf{\Pi}_{68 \times 68}$ is non-negative. The last state O_{31} in the old stage is as an absorbing state in the Markov chain process, meaning that the matrix $\mathbf{\Pi}$ is reducible. In order to characterise the equilibrium distribution of the population (as well to study parameter estimation) an irreducible transition matrix is needed. Thus, consider the following vector representation of the system

$$Y(t + 1) = \widetilde{\mathbf{\Pi}}Y(t) \quad (3.3.a)$$

$$O(t + 1) = \Psi O(t) + a(Y(t)), \quad (3.3.b)$$

where Y is the vector of states from which old individuals are deleted, $\widetilde{\mathbf{\Pi}}$ is the sub-matrix of $\mathbf{\Pi}$ in which all rows and columns concerning the dynamics of old individuals, (i.e., the last row-block and column-block in (3.2)) are deleted. The function $a(\cdot)$ is

vector-valued that takes the form:

$$a(Y(t)) = \begin{pmatrix} (1 - \alpha)s_{I_{18}}I_{18}(t) + s_{R_{18}}R_{18}(t) \\ s_{R_{19}}R_{19}(t) + (1 - \beta)s_{M_{19}}M_{19}(t) \\ s_{R_{20}}R_{20}(t) \\ 0 \\ \vdots \\ 0 \end{pmatrix} \quad (3.4)$$

and Ψ is the following matrix:

$$\Psi = \begin{pmatrix} 0 & 0 & \dots & 0 \\ s_{O_{19}} & 0 & \dots & 0 \\ 0 & s_{O_{20}} & \dots & 0 \\ & & \ddots & \\ 0 & 0 & \dots & s_{O_{30}} \end{pmatrix}. \quad (3.5)$$

with this notation, matrix $\tilde{\Pi}$ (3.6) is irreducible, but still is non-negative and square (with dimension 53×53),

$$\tilde{\Pi} = \begin{pmatrix} [J \rightarrow J] & 0 & 0 & [R \rightarrow J] & 0 \\ [J \rightarrow I] & [I \rightarrow I] & 0 & 0 & 0 \\ 0 & [I \rightarrow M] & [M \rightarrow M] & 0 & [P \rightarrow M] \\ 0 & 0 & [M \rightarrow R] & 0 & [P \rightarrow R] \\ 0 & 0 & 0 & [R \rightarrow P] & [R \rightarrow P] \end{pmatrix}. \quad (3.6)$$

As discussed, $\tilde{\Pi}$ is formed by eliminating all transitions related to the old stage. Therefore, to describe the dynamic of the population, only the behaviour of individuals of ages 1 to 21 are taken into account since individuals older than 21 all belong to the old stage.

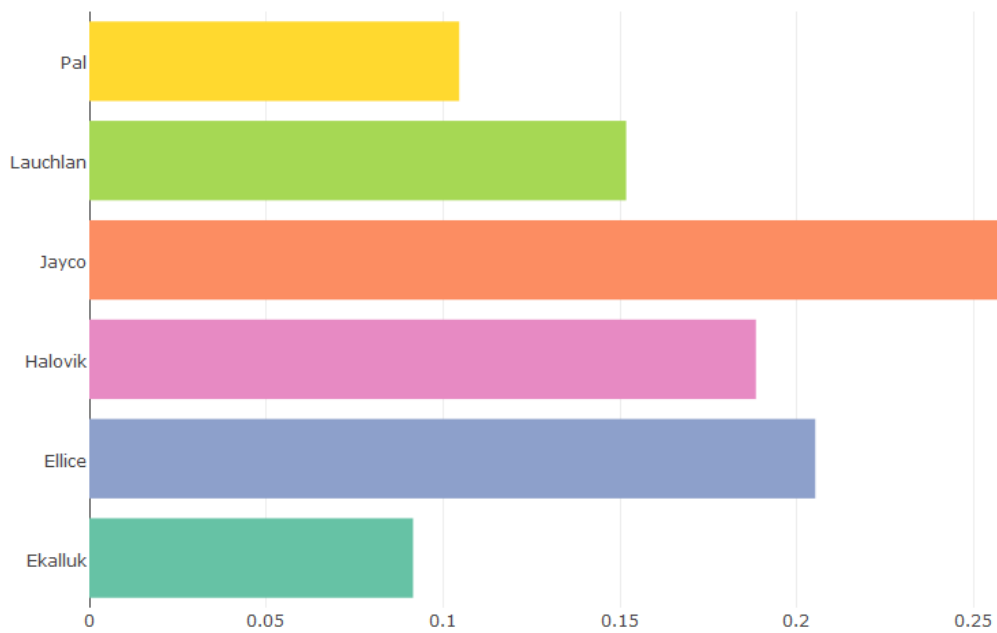


Figure 3.3: Data frequency collected from six fishing sites; Pal, Lauchlan, Jayco, Halovik, Ellice and Ekalluk.

3.2 Data structure

In late 1940s, the Shaw Steamship Company harvested (using gill-nets) a large amount of fish, marking the beginning of commercial wild Arctic Charr fishing. Weirs were implemented as the second type of fishing method in 1994. Since 1971, Fisheries and Oceans Canada takes samples among the commercially harvested fish in order to study the impact of fishing on Arctic Charr populations. The available data for the current study was collected annually from 1972 to 2009 on fishing sites located at the mouth of 6 rivers: Lauchlan, Halovik, Paliryuak, Ekallik, Ellice and Jayco (Figure 3.3).

Each year, from 60 to 1200 individuals were collected (650 individuals on average). As this collection proceeds after fish are processed on the boats, individuals have usually been prepared and thus lack their sexual organs, making the determination of sex impossible in most cases. Length, emptied weight and age are recorded. Some sampling campaigns were conducted with the objective of acquiring more data, such as sex, true weight, sexing as objectives, but most data lacks it. The time series is

3.2. DATA STRUCTURE

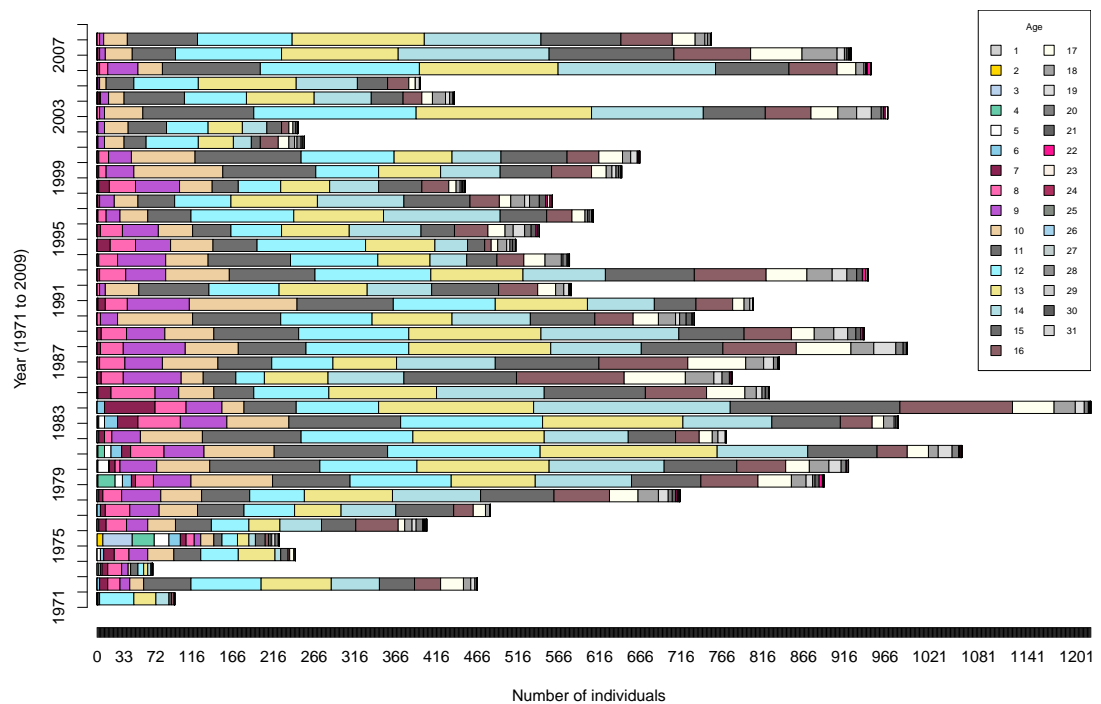


Figure 3.4: Number of individuals collected per year from 1971 to 2009, with indication of the numbers of individuals in each age class. Note that data that does not have any information about age is eliminated.

extensive, providing data about 48,900 individuals over a time period spanning 1971 to 2009 (Figure 3.4).

Age was established for 25,460 of these individuals, which is used as the basis for analysis. Given the restriction of information on sex of captured individuals, the population is assumed to be one sex (all female). Also, we tried to solve the parameter estimation problem with considering only the half of the population (as female population), which in that case the result was not different from assuming a unisex population. In addition, in this preliminary work, spatial movement of individuals is not considered. Moreover, the fishing methods have led to sample bias due to the fact that both methods use 140 mm mesh size. Therefore, individuals of small size cannot be captured by those methods [61]. As a result, the number of individuals of age 12 or less in the available data is much lower than older individuals and a normal distribution for population appears over age classes (Figure 3.5). However, a decreasing function of age is expected for the total population of Arctic Charr due to the high mortality of

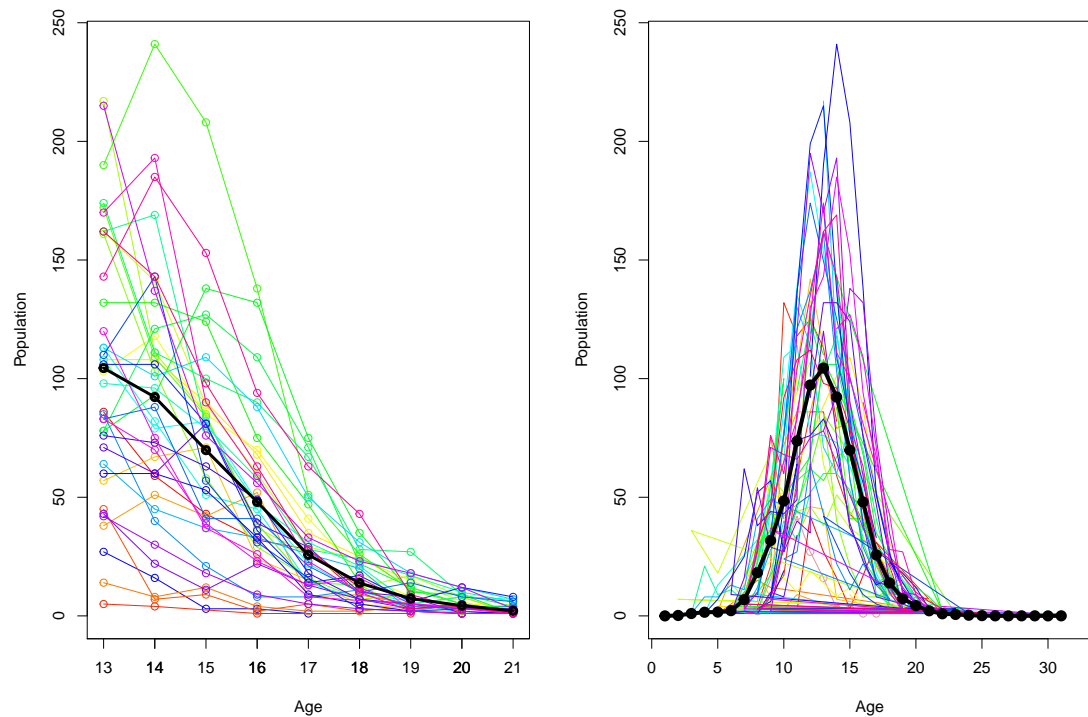


Figure 3.5: Age distribution of the population for 39 years of observations, with the average number of individuals in each age class shown as a thick black line.

Arctic Charr in the early ages. In practice, data on population of age 5 or less are not reliable (Figure 3.6).

To address this problem, a linear regression is used to estimate the population of individuals younger than 13 years old. The logarithm of the reliable part of the available data (i.e., the population of ages 13 and older) is used to fit a regression line and then the corresponding number of individuals of ages 12 and younger are estimated based on this fit. Note that assuming a constant motility across age and years, an decreasing exponential form for the population is expected (with respect to age). Therefore, using the logarithm values we have the graph of population as a straight line, so we use the regression method to estimate the missing part of data (number of individuals of early ages). Therefore, a combination of real data (ages 13 to 21) and estimated data (1 to 12 years old) is used. In fact, this estimation dramatically increased the sample size from 48,937 to 21,175,761. This huge difference can be interpreted as the high number of off-spring and individuals in the juvenile stage that were not measurable by

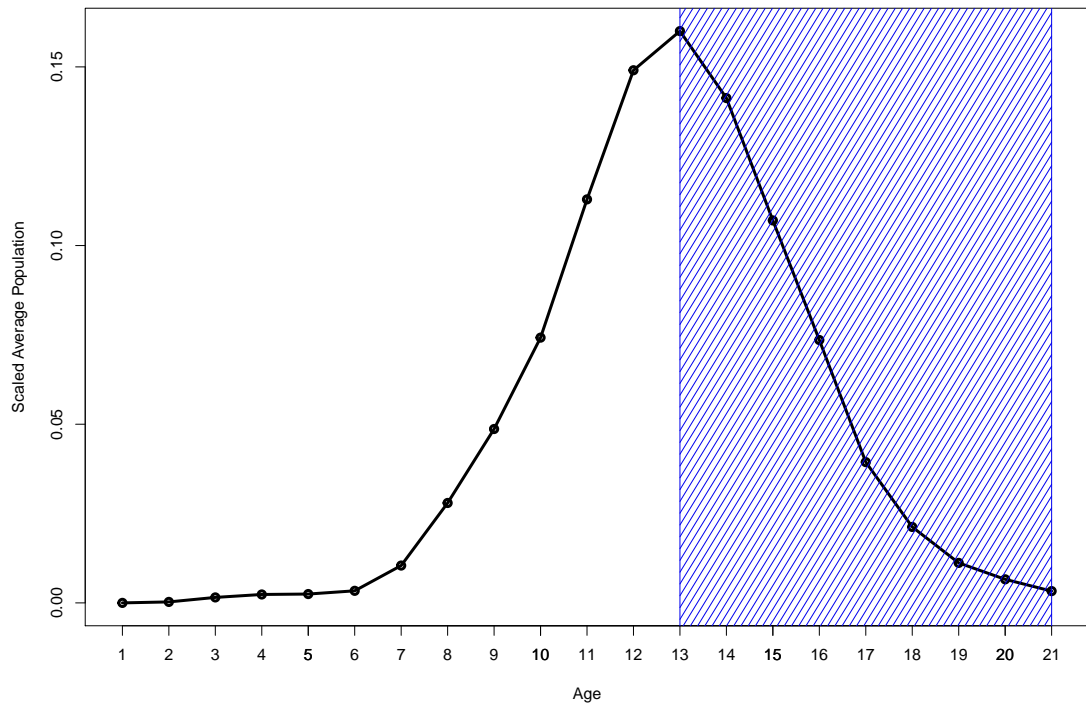


Figure 3.6: Average population distributions in 39 years of observations. The shaded area indicates the range of reliable data.

implemented sampling methods.

In the following section, both sets of data are considered (incomplete available data and estimated data) to find the set of parameters providing the best fit to the mathematical model (3.1).

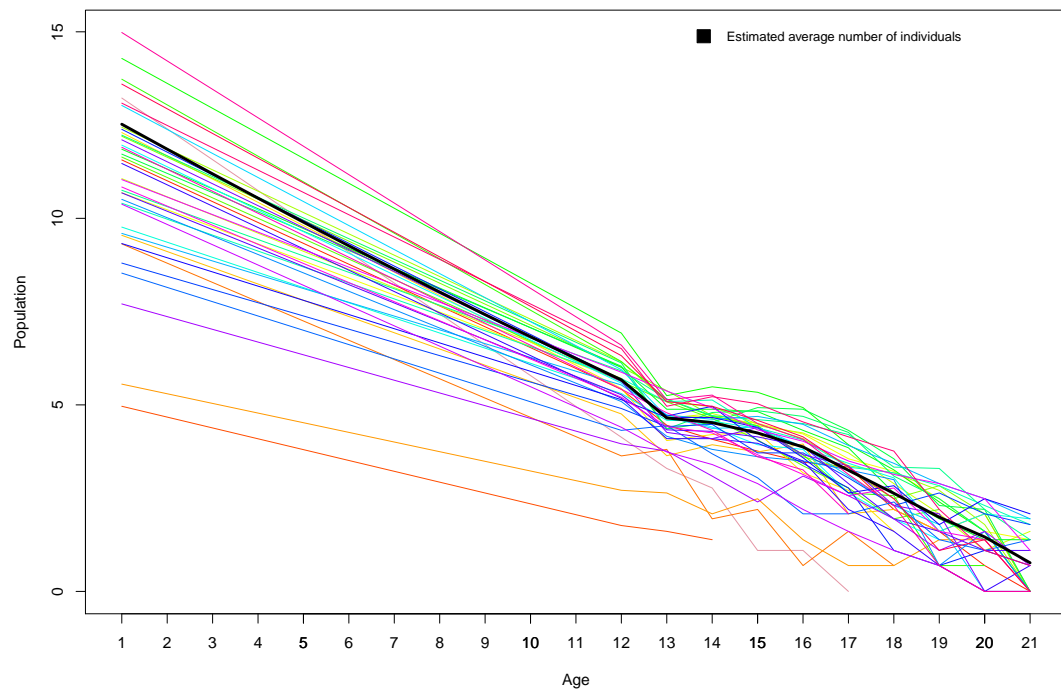


Figure 3.7: Age distribution of population for 39 years of observations, with the average number of individuals in each age class shown as a thick black line. Note that a logarithmic estimation for the number of individuals younger than 13 years old is considered instead of available data.

3.3 Parameter estimation

The model in Section 3.1 has 68 parameters. Such a high number of parameters leads to an unidentifiable parameter estimation problem. Therefore, to obtain an identifiable model, we adjust the model by re-parametrizing it. We assume that all fish in same stage have the same chance to survive independently of their age. Thus, we group parameters corresponding to stage survival rates. This adjustment reduces the number of parameters to 10 and results in more accurate estimation. The new set of parameters consists of $S_J, S_I, S_M, S_R, S_P, S_O, \alpha, \beta, \gamma$ and f .

The purpose of this section is to solve the inverse problem for the model, i.e., to fit a parameter-sparse model to the observed data. Data is summarized by fish age for the entire period of study (1971 to 2009), giving a vector with the number of observed individuals for each age. As discussed above, only individuals of age between 13 and 21 years can be considered from the original set of data; later on we discuss the results using the completed set of data that is formed in Section 5.2. Data points are denoted $n_0 = \langle d_{13}, d_{14}, \dots, d_{21} \rangle$. This vector is compared to $\delta = \langle \delta_{13}, \delta_{14}, \dots, \delta_{21} \rangle$ obtained by computing the equilibrium distribution for the model, with $\delta_i = I_i^* + M_i^* + R_i^* + P_i^*$ for $i = 13, \dots, 18$, $\delta_{19} = M_{19}^* + R_{19}^* + O_{19}^*$, $\delta_{20} = R_{20}^* + O_{20}^*$ and $\delta_{21} = O_{21}^*$.

A classical technique, ordinary least squares (OLS), minimises the error

$$\arg \min \sum_{i=14}^{21} (d_i - \delta_i)^2. \quad (3.7)$$

Ordinary least square is a linear approach. Implementing this method requires certain assumptions. In [6], five important assumptions are listed:

- The linear regression model is *linear in parameters*.
- There is a random sampling of observations.
- There is no multi-collinearity (or perfect collinearity), i.e., there is no linear relationship between independent variables.

- Error terms are normally distributed, i.e., the distribution of error terms has zero mean and does not depend on the independent variables. Note that only the error terms need to be normally distributed; the dependent variable Y need not be normally distributed.
- Independent and identically distributed (i.i.d.) error terms (having expected value zero and constant variance).

Consider the error terms of the population estimation as $\varepsilon_i = d_i - \delta_i$ and constant variance of error terms as σ^2 , then the last assumption implies three other characteristics for error terms.

1. The conditional mean should be zero, i.e., the expected value of the mean of the error terms of OLS regression should be zero given the values of independent variables, i.e.,

$$E(\varepsilon_i) = 0.$$

2. No autocorrelation, i.e.,

$$\text{Cov}(\varepsilon_i, \varepsilon_j) = 0 \quad \text{for } i \neq j.$$

3. Homoscedasticity, i.e.,

$$\text{var}(\varepsilon_i) = \sigma^2 \quad \text{for all } i.$$

Violation of this last condition, i.e. $\sigma_i^2 \neq \sigma_j^2$ for $i \neq j$, leads to *heteroscedasticity*. In the presence of heteroscedasticity, the OLS estimation is biased and even increasing the number of observations cannot address this problem. To examine the presence of i.i.d. and homoscedasticity, plotting the residuals is a common technique. Since it is assumed that the errors are i.i.d., a plot of the residuals against time and estimated values of the model should both be random (and neither increasing nor decreasing with respect to time). If not, then the constant variance assumption is suspect. We present scatter plots of residuals against time (Figure 3.8) and estimated value for the

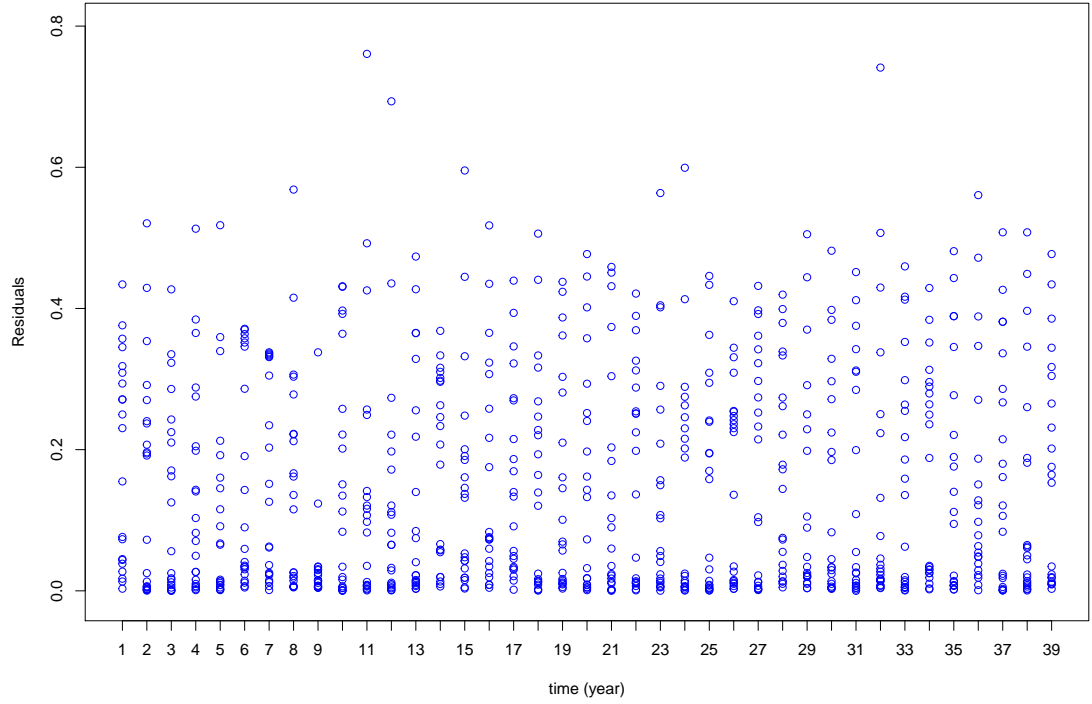


Figure 3.8: Scatter plot of residuals versus time for the OLS method.

population (Figure 3.9). The increasing and non-random trend of the second plot indicates heteroscedasticity and consequently the lack of the i.i.d property of the data set. In the absence of i.i.d. errors, a common weighted error method, in which the error is weighted, can be a good substitute for the OLS method. This method is called weighted least squares (WLS) and its assumptions are more reasonable when data varies widely in the scale of observations. The WLS estimate can be thought of as minimizing the distance between data and model while taking into account the known but unequal quality of the observations; we minimize:

$$\arg \min \sum_{i=14}^{21} \frac{1}{w_i^2} (d_i - \delta_i)^2. \quad (3.8)$$

The nature of the problem imposes some restrictions on the inverse parameter estimation problem. First, based on the definition of the parameters, it is desirable to have all survival rates ($S_J, S_I, S_M, S_R, S_P, S_O$) and rates of between stage transition (α, β, γ) in $[0, 1]$. As discussed in Section 5.2, the number of individuals is supposed to be a

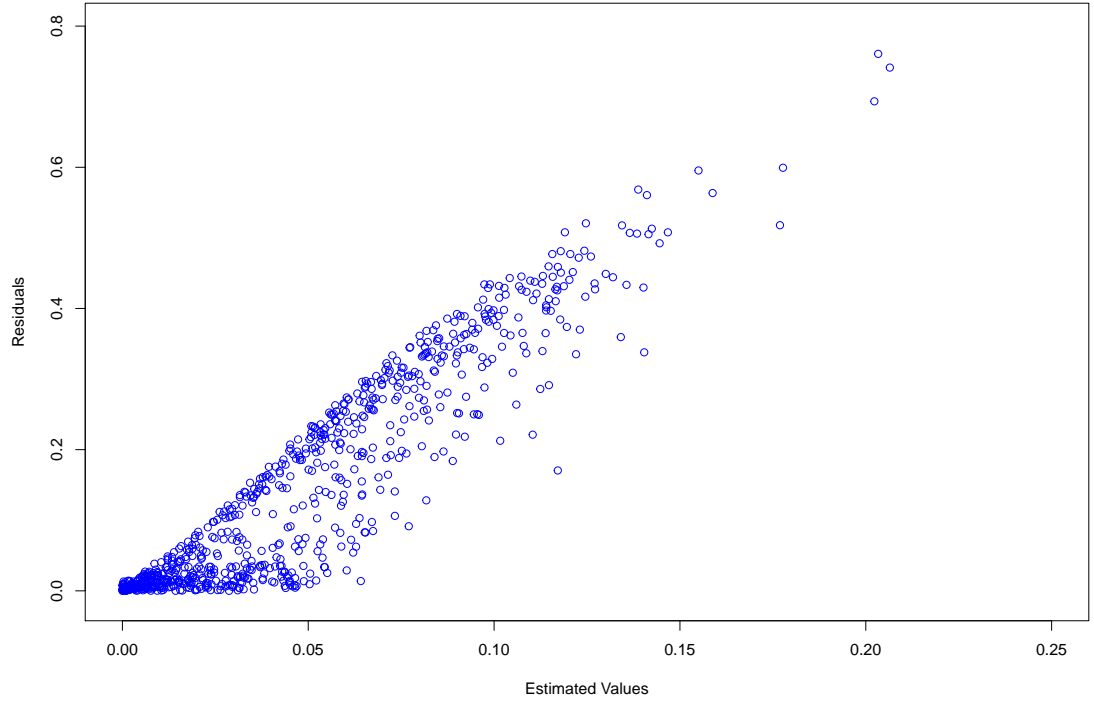


Figure 3.9: Scatter plot of residual versus population distribution which were estimated with the WLS method.

decreasing function of age. Therefore, in order to keep parameters realistic, a penalty is applied to the error term when estimated parameters result in increasing population for ages 17 and older. Also, the fertility parameter f is assumed to be fixed (3500). Therefore, the generalized weighted least square method is formed as follows:

$$\arg \min \varepsilon = 8\varepsilon_1 + 10\varepsilon_2, \quad (3.9)$$

where ε_1 and ε_2 are defined as:

$$\varepsilon_1 = \sum_{i=14}^{21} \frac{1}{w_i^2} (d_i - \delta_i)^2, \quad (3.10a)$$

$$\varepsilon_2 = \begin{cases} 0 & \text{Decreasing distribution for } 17 \leq i \leq 21 \\ 1 & \text{Increasing distribution for } 17 \leq i \leq 21. \end{cases} \quad (3.10b)$$

Note that the coefficients of the error terms (8 and 10) were chosen by trying many sets of numbers. In order to solve the above mentioned optimization problem (minimizing

the error term), we utilize islands genetic algorithms (ISLGAs)¹. Indeed, to implement the optimization we use a predefined package in *R*. Since the model parameters are supposed to be representations of real numbers we use the *real-value* type of function. We implement the optimization in two steps. First, we consider the weights as a set of parameters and estimate them with the same genetic algorithm method. Then, in the second step we fix the best weights (consider them as constants) and estimate the vector of ten parameters. The result of parameter estimation is summarized in Table 3.1 with weights

$$W = \langle 0.26, 0.50, 0.60, 0.80, 0.50, 0.37, 0.65, 0.77, 0.53 \rangle. \quad (3.11)$$

The graph of the estimated age distribution versus the age distribution of the average

Parameter	Parameter description	Estimated value
S_J	Juvenile survival	0.626
S_I	Immature survival	0.774
S_M	Mature survival	0.466
S_R	Reproducing survival	0.495
S_P	Post-reproducing survival	0.288
S_O	Old survival	0.571
α	Transition from immature to mature	0.498
β	Transition from mature to reproducing	0.839
γ	Transition from post-repro to reproducing	0.212
f	Fertility*	3500

Table 3.1: Estimated parameter values using weighted least squares method. (*The value for fertility is not estimated by the parameter estimation method.)

of the observed population is plotted in Figure 3.10. The incomplete data set led to poor estimation for the population younger than 13 years old. So, we only considered the dynamics of the population older than 13 years old. The lowest survival rate is estimated for the individuals in the post-reproducing stage ($S_P = 0.288$): at the end of each year, only about one quarter of them survive. This could be the result of passing through the high demand reproduction process which is then followed by high

¹Independent GAs are executed in each island, and only occasionally sparse exchanges of individuals are performed among the islands. In principle islands can evolve sequentially, but increased computational efficiency is obtained by running GAs in parallel on each island.

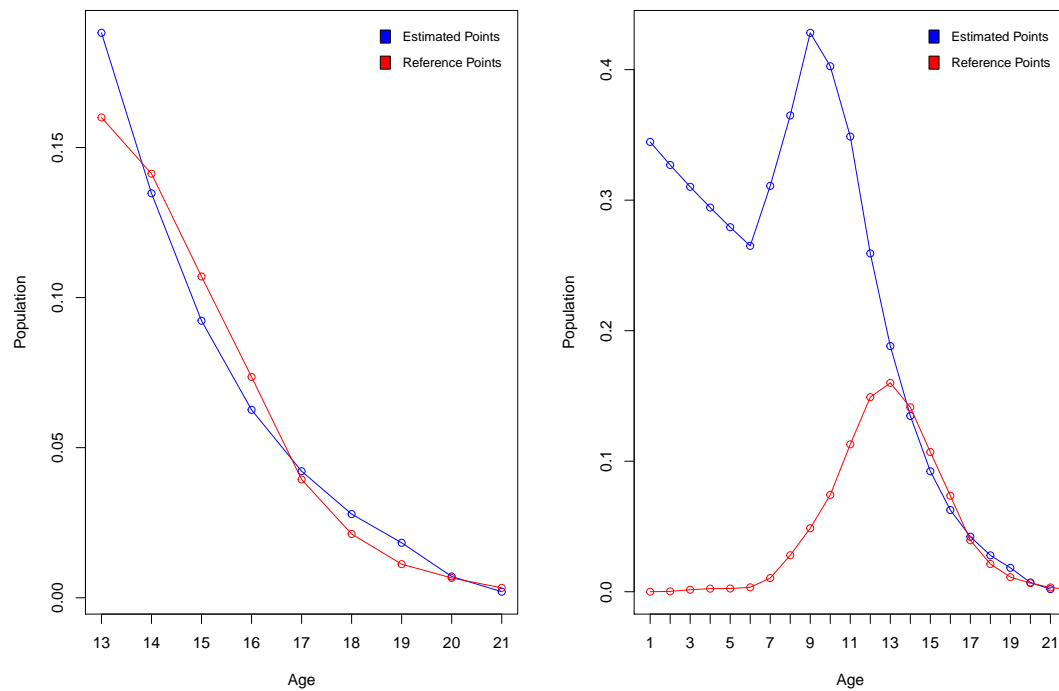


Figure 3.10: Estimated population distribution and data points. The red curve illustrates the age distribution of mean population and the blue curve presents the estimated age distribution.

mortality during the winter, which is extremely cold and as a result the access to the food sources is very limited. Individuals in the mature and reproducing stages have almost the same survival rates of about 40% ($S_M = 0.466$, $S_R = 0.495$) each year. For mature individuals, this may be interpreted as a consequence of migration, which starts when individuals move to the mature stage where they experience huge environmental changes.

Given the estimated parameters, about 50% of immature individuals become mature by the end of each year ($\alpha = 0.498$). Also, about 80% of mature individuals reproduce in the following year, while 20% of the post-reproductive individuals reproduce again, so 80% wait for at least one year before their next reproduction ($\gamma = 0.212$). Parameter estimation also revealed that, annually, about 20% of individuals that have never reproduced move from the mature stage to the old stage.

3.4 Characteristics of the population deduced from $\tilde{\Pi}$

In this section, we focus on that part of the mathematical model that is described by the irreducible transition matrix in (3.6). Excluding the old stage has led to $\tilde{\Pi}$ being an irreducible matrix. Also, this matrix is primitive with primitivity index 33, i.e., $\tilde{\Pi}^{33} > 0$, where the notation > 0 indicates a strongly positive matrix, i.e., one which has all its entries positive (the same notation is used for vectors). The primitivity index of $\tilde{\Pi}$ can also be interpreted biologically: it takes 33 years until a newborn individual (J_0) and its descendants can potentially be in any of the state of system. This property is crucial to characterizing the long term behaviour of the population. In the following, we discuss the long run behaviour of the population, mostly based on the properties of the transition matrix $\tilde{\Pi}$.

3.4.1 Population growth rate λ_1

Primitivity of $\tilde{\Pi}$ provides sufficient conditions for the Perron-Frobenius theorem (Theorem 2.1), which guarantees the existence of a real and positive dominant eigenvalue. As discussed in Section 2.2, this eigenvalue can be interpreted as the geometric rate of growth of the population.

We evaluated λ_1 for the transition matrix $\tilde{\Pi}$ as 0.66. This value describes a decreasing behaviour for the population in the long run, i.e., the population is expected to become extinct eventually. This expectation of extinction might be explained as a consequence of our assumption of experiencing a constant environment, the current harvesting amount or even assuming a constant fertility for different ages.

3.4.2 Ergodicity

Given the definition of allowable matrices (Definition 2.5) and the primitivity and non-negativity of $\tilde{\Pi}$, the matrix $\tilde{\Pi}$ is allowable. Also, referring to the definition of ergodic sets (Definition 2.6), we can consider $\{\tilde{\Pi}\}$ as an ergodic set. Thus, $\tilde{\Pi}$ is ergodic in the weak sense based on Theorem 2.4. Therefore, a tendency for the age distribution to be

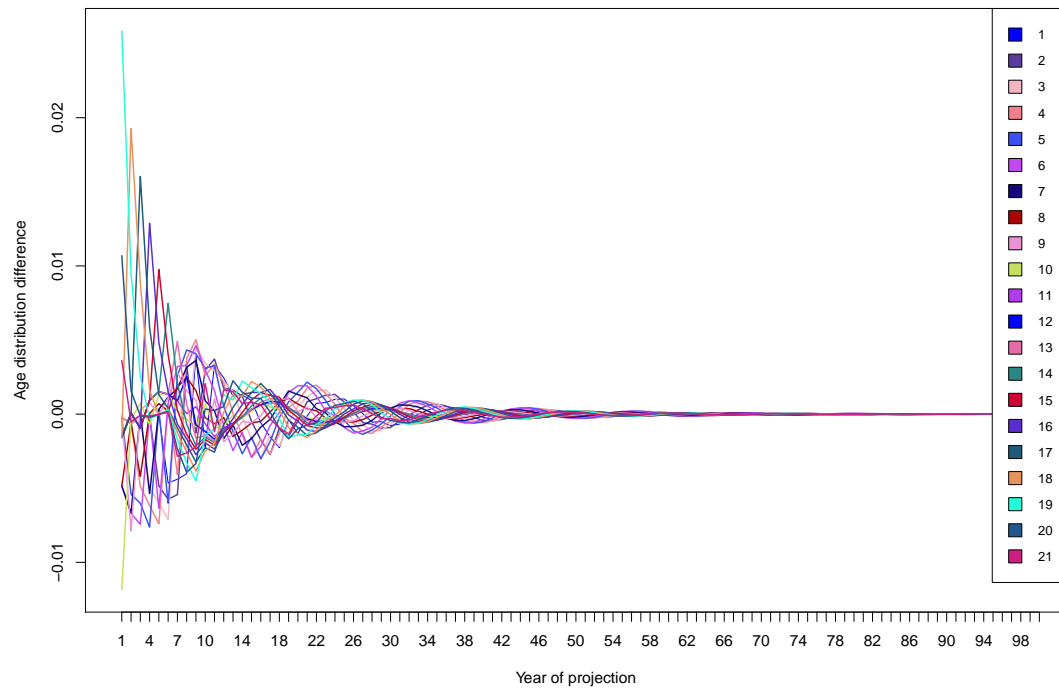


Figure 3.11: Difference between age distributions of the population simulated over 100 years. Weak ergodicity guarantees a tendency towards age distribution proportionality in the long run.

similar in the long run is expected, with the age distribution not necessarily approaching a limiting distribution. In Figure 3.11, the difference between age distributions over 100 years is simulated. Each curve is related to one age group and represents the fluctuations of this age group's share of the total population over 100 years. This reveals that after about 60 years the difference between age distributions from one year to the next year is almost zero, i.e., as we expect from the ergodic behaviour of the population in weak sense, a tendency towards having age distribution proportionality appears in the long run. Also, to illustrate the ergodic behaviour of the population, we utilized 4 different age distribution vectors as initial conditions to project the population forward 100 years. The result are presented in Figure 3.12. It is evident that, in the long run, the population behaves independently of the initial age distribution.

3.4. CHARACTERISTICS OF THE POPULATION DEDUCED FROM $\tilde{\Pi}$

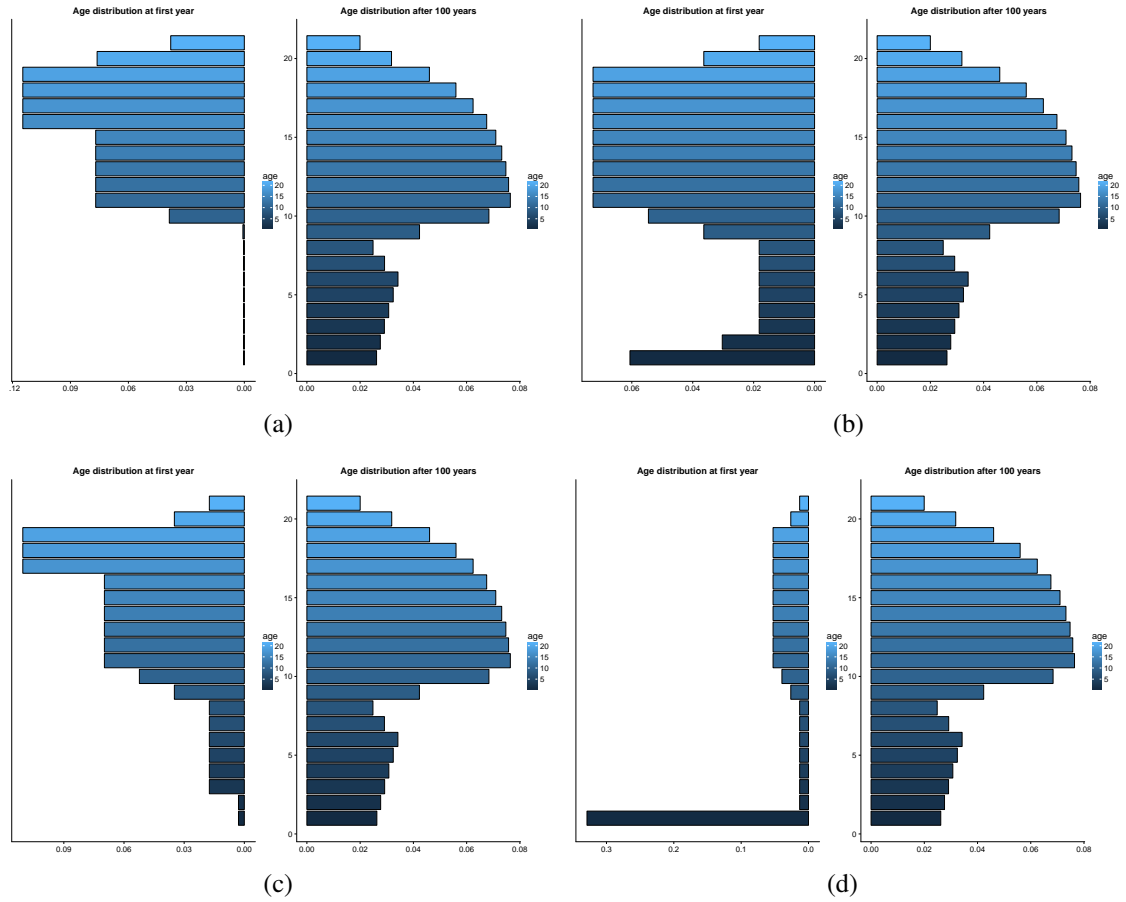


Figure 3.12: Illustration of the consequence of weak ergodicity. Each figure has on the left an initial distribution of individuals in age classes and on the right, the distribution of individuals in age classes after 100 years.

3.5 Sensitivity analysis

In order to assess the effects of any perturbation in initial conditions or parameters on the mathematical model, we implement a sensitivity analysis as discussed in Section 2.2. We seek the sensitivities of the Perron-Frobenius eigenvalue (the dominant eigenvalue) to changes in the parameters of the model. We start with the sensitivity of λ to small perturbations in elements of $\tilde{\mathbf{\Pi}}$, where (i, j) -th entry is denoted a_{ij} for $i, j = 1, \dots, 53$. Since the eigenvalues are functions of a_{ij} that are implicitly expressed in the characteristic equation

$$\det(\tilde{\mathbf{\Pi}} - \lambda I) = 0, \quad (3.12)$$

we use implicit differentiation to find $\partial\lambda/\partial a_{ij}$. This is known as sensitivity of λ to a_{ij} [18, 20, 32, 33]. Thus, we introduce the sensitivity matrix S , with (i, j) -th entry representing the sensitivity of λ to changes in a_{ij} , i.e.,

$$s_{ij} = \partial\lambda/\partial a_{ij}. \quad (3.13)$$

Then, let w and v be the right and left eigenvectors corresponding to λ [7]:

$$\tilde{\mathbf{\Pi}}w = \lambda w \quad (3.14a)$$

$$v^* \tilde{\mathbf{\Pi}} = \lambda v^*, \quad (3.14b)$$

where $*$ is the complex conjugate transpose (note that we work with the Perron-Frobenius real eigenvalues and vectors, so here $*$ is just a transpose). Differentiating both sides of equation (3.14a), we have the following formula for λ sensitivities:

$$s_{ij} = \frac{\bar{v}_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle}. \quad (3.15)$$

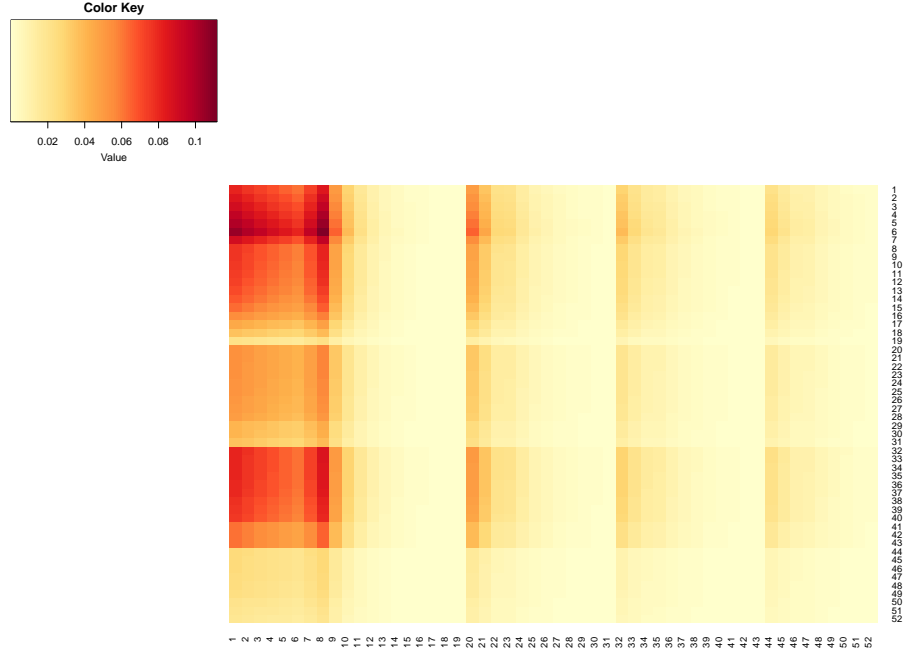


Figure 3.13: This heat map illustrates the sensitivity of λ to perturbations in the transition matrix elements. The relation between colours and values of sensitivity is shown in the colour key.

This value is proportional to the product of i th element of reproductive value vector (v_i) and the j th element of the stable stage distribution vector (w_j). Therefore, we have:

$$S = \frac{\mathbf{v}\mathbf{w}^T}{\mathbf{v}^T\mathbf{w}}. \tag{3.16}$$

The heat map in Figure 3.13 provides a visual of the sensitivity of λ to perturbations in the transition matrix $\tilde{\mathbf{\Pi}}$ entries. Looking at the left side of the heat map, the majority of cells are in the red to orange range. This indicates a high sensitivity of λ to perturbations, for transitions of young individuals (individuals in the juvenile and immature stages). Also, as we move from the left to the right side of the heat map, cell colours turn lighter (from dark red to pale yellow), which reveals lower sensitivity of the growth rate to perturbations in transitions related to individuals in the mature, reproducing and post-reproducing stages.

However, having both age- and stage-structure in our model reduces the explanatory power of the sensitivity matrix S , which only describes the sensitivities of λ to the entries of $\tilde{\mathbf{\Pi}}$. Thus, we also look for sensitivity to the parameters of the model to

provide a more precise explanation of the λ 's sensitivity. To do so, we utilize the chain rule and differentiate the corresponding elements in $\tilde{\Pi}$.

To do so, we utilize the chain rule and differentiate the corresponding elements in $\tilde{\Pi}$. Thus, the sensitivities of λ to model parameters are as follows:

$$\frac{\partial \lambda}{\partial s_J} = \sum_{i=2}^7 s_{i,(i-1)}, \quad (3.17a)$$

$$\frac{\partial \lambda}{\partial s_I} = s_{7,6} + s_{8,7} + (1 - \alpha) \sum_{i=9}^{19} s_{i,(i-1)} + \alpha \sum_{i=20}^{31} s_{i,(i-12)}, \quad (3.17b)$$

$$\frac{\partial \lambda}{\partial s_M} = (1 - \beta) \sum_{i=21}^{31} s_{i,(i-1)} + (\beta) \sum_{i=32}^{43} s_{i,(i-12)}, \quad (3.17c)$$

$$\frac{\partial \lambda}{\partial s_R} = \sum_{i=44}^{52} s_{i,(i-12)}, \quad (3.17d)$$

$$\frac{\partial \lambda}{\partial s_P} = (1 - \gamma) \sum_{i=23}^{31} s_{i,(i+21)} + \gamma \sum_{i=34}^{42} s_{i,(i+10)}, \quad (3.17e)$$

$$\frac{\partial \lambda}{\partial \alpha} = s_I \sum_{i=20}^{31} s_{i,(i-12)} - s_I \sum_{i=9}^{19} s_{i,(i-1)}, \quad (3.17f)$$

$$\frac{\partial \lambda}{\partial \beta} = s_M \sum_{i=32}^{43} s_{i,(i-12)} - s_M \sum_{i=21}^{31} s_{i,(i-1)}, \quad (3.17g)$$

$$\frac{\partial \lambda}{\partial \gamma} = s_P \sum_{i=34}^{42} s_{i,(i+10)} - s_P \sum_{i=23}^{31} s_{i,(i+21)}, \quad (3.17h)$$

$$\frac{\partial \lambda}{\partial f} = \sum_{i=32}^{43} s_{1,(i+1)}. \quad (3.17i)$$

It is evident that the sensitivity of λ to s_I depends on α ; also $\partial \lambda / \partial s_M$ is a function of β and $\partial \lambda / \partial s_P$ is itself a function of γ . Also, we have the same issue for $\partial \lambda / \partial \alpha$, $\partial \lambda / \partial \beta$, $\partial \lambda / \partial \gamma$, which are dependent on s_I , s_M and s_P . To address this issue, first the values of the independent parameters in each case are fixed and then the values of the sensitivities are calculated and the results are summarized in Table 3.2. The highest sensitivities, as it was expected, are related to survival in the juvenile and immature stages and the lowest one is related to transition from reproducing to post-reproductive stage. Also, changes in α have a negative impact on the rate of growth, which can be explained using the results of the parameter estimation in Table 3.1. Indeed, the

3.5. SENSITIVITY ANALYSIS

λ Sensitivity to	Dependent on	Parameter value	Sensitivity
S_J	-	-	0.4964
S_I	α	0.498	0.3023
S_M	β	0.840	0.1566
S_R	-	-	0.0321
S_P	γ	0.213	0.0552
α	S_I	0.775	-0.0397
β	S_M	0.466	0.0263
γ	S_P	0.288	0.0076

Table 3.2: Sensitivity of λ to perturbation in model parameters. Given the dependence of a number of sensitivities on other parameters, the best estimated parameter value (third column) is used to calculate the sensitivities in the last column.

lowest survival rate (0.212) is estimated for individuals in the post-reproductive stage. Therefore, any increase in the value of α (which is the rate of transition to the post-reproductive stage) leads to a decrease of the total population, i.e., more individuals move to a high risk stage when the value of α increases, which has a negative effect on the rate of growth. Given the fact that first-order sensitivities of λ to some parameters of the model are not constant, it is interesting to discuss second-order sensitivities.

Second-order sensitivities of λ to the parameters $s_I, s_M, s_P, s_\gamma, s_\alpha$ and s_β , are obtained by differentiating first-order sensitivities with respect to parameters α, β and γ . Note that the sensitivities $\partial\lambda/\partial s_J, \partial\lambda/\partial s_R$ are independent of other variables, also we assume that the parameters of the model are independent, so no second-order sensitiv-

ities are required for them. Second-order sensitivities take the form

$$\begin{aligned}\frac{\partial^2 \lambda}{\partial s_I \partial \alpha} &= \frac{\partial^2 \lambda}{\partial a_{7,6} \partial \alpha} + \frac{\partial^2 \lambda}{\partial a_{8,7} \partial \alpha} - \sum_{i=9}^{19} s_{i,(i-1)} + (1 - \alpha) \sum_{i=9}^{19} \frac{\partial^2 \lambda}{\partial a_{i,(i-1)} \partial \alpha} + \sum_{i=20}^{31} s_{i,(i-12)} \\ &+ \alpha \sum_{i=20}^{31} \frac{\partial^2 \lambda}{\partial a_{i,(i-12)} \partial \alpha}, \\ \frac{\partial^2 \lambda}{\partial s_M \partial \beta} &= - \sum_{i=21}^{31} s_{i,(i-1)} + (1 - \beta) \sum_{i=21}^{31} \frac{\partial^2 \lambda}{\partial a_{i,(i-1)} \partial \beta} + \sum_{i=32}^{43} s_{i,(i-12)} + \beta \sum_{i=32}^{43} \frac{\partial^2 \lambda}{\partial a_{i,(i-12)} \partial \beta}, \\ \frac{\partial^2 \lambda}{\partial s_P \partial \gamma} &= - \sum_{i=23}^{31} \frac{\partial^2 \lambda}{\partial a_{i,(i+21)} \partial \beta} + (1 - \gamma) \sum_{i=23}^{31} s_{i,(i+21)} + \sum_{i=34}^{42} s_{i,(i+10)} + \gamma \sum_{i=34}^{42} \frac{\partial^2 \lambda}{\partial a_{i,(i+10)} \partial \beta},\end{aligned}$$

or equivalently,

$$\begin{aligned}\frac{\partial^2 \lambda}{\partial \alpha \partial s_I} &= \sum_{i=20}^{31} s_{i,(i-12)} + s_I \sum_{i=20}^{31} \frac{\partial^2 \lambda}{\partial a_{i,(i-12)} \partial s_I} - \sum_{i=9}^{19} s_{i,(i-1)} - s_I \sum_{i=9}^{19} \frac{\partial^2 \lambda}{\partial a_{i,(i-1)} \partial s_I}, \\ \frac{\partial^2 \lambda}{\partial \beta \partial s_M} &= \sum_{i=32}^{43} s_{i,(i-12)} + s_M \sum_{i=32}^{43} \frac{\partial^2 \lambda}{\partial a_{i,(i-12)} \partial s_M} - \sum_{i=21}^{31} s_{i,(i-1)} - s_M \sum_{i=21}^{31} \frac{\partial^2 \lambda}{\partial a_{i,(i-1)} \partial s_M}, \\ \frac{\partial^2 \lambda}{\partial \gamma \partial s_P} &= \sum_{i=34}^{42} s_{i,(i+10)} + s_P \sum_{i=34}^{42} \frac{\partial^2 \lambda}{\partial a_{i,(i+10)} \partial s_P} - \sum_{i=23}^{31} s_{i,(i+21)} - s_P \sum_{i=23}^{31} \frac{\partial^2 \lambda}{\partial a_{i,(i+21)} \partial s_P}.\end{aligned}$$

Then, using chain rule again to differentiate we can expand the formulas of second-

order sensitivities are as follows:

$$\begin{aligned}
 \frac{\partial^2 \lambda}{\partial s_I \partial \alpha} &= \sum_{p,q=1}^{52} \frac{\partial a_{p,q}}{\partial \alpha} \frac{\partial^2 \lambda}{\partial a_{7,6} \partial a_{p,q}} + \sum_{p,q=1}^{52} \frac{\partial a_{p,q}}{\partial \alpha} \frac{\partial^2 \lambda}{\partial a_{8,7} \partial a_{p,q}} - \sum_{i=9}^{19} s_{i,(i-1)} \\
 &+ (1 - \alpha) \sum_{i=9}^{19} \left(\sum_{p,q=1}^{52} \frac{\partial a_{p,q}}{\partial \alpha} \frac{\partial^2 \lambda}{\partial a_{i,(i-1)} \partial a_{p,q}} \right) + \sum_{i=20}^{31} s_{i,(i-12)} + \alpha \sum_{i=20}^{31} \left(\sum_{p,q=1}^{52} \frac{\partial a_{p,q}}{\partial \alpha} \frac{\partial^2 \lambda}{\partial a_{i,(i-12)} \partial a_{p,q}} \right), \\
 \frac{\partial^2 \lambda}{\partial s_M \partial \beta} &= - \sum_{i=21}^{31} s_{i,(i-1)} + (1 - \beta) \sum_{i=21}^{31} \left(\sum_{p,q=1}^{52} \frac{\partial a_{p,q}}{\partial \beta} \frac{\partial^2 \lambda}{\partial a_{i,(i-1)} \partial a_{p,q}} \right) + \sum_{i=32}^{43} s_{i,(i-12)} \\
 &+ \beta \sum_{i=32}^{43} \left(\sum_{p,q=1}^{52} \frac{\partial a_{p,q}}{\partial \beta} \frac{\partial^2 \lambda}{\partial a_{i,(i-12)} \partial a_{p,q}} \right), \\
 \frac{\partial^2 \lambda}{\partial s_P \partial \gamma} &= - \sum_{i=23}^{31} \left(\sum_{p,q=1}^{52} \frac{\partial a_{p,q}}{\partial \gamma} \frac{\partial^2 \lambda}{\partial a_{i,(i+21)} \partial a_{p,q}} \right) + (1 - \gamma) \sum_{i=23}^{31} s_{i,(i+21)} + \sum_{i=34}^{42} s_{i,(i+10)} \\
 &+ \gamma \sum_{i=34}^{42} \left(\sum_{p,q=1}^{52} \frac{\partial a_{p,q}}{\partial \gamma} \frac{\partial^2 \lambda}{\partial a_{i,(i+10)} \partial a_{p,q}} \right),
 \end{aligned}$$

or equivalently,

$$\begin{aligned}
 \frac{\partial^2 \lambda}{\partial \alpha \partial s_I} &= \sum_{i=20}^{31} s_{i,(i-12)} + s_I \sum_{i=20}^{31} \left(\sum_{p,q=1}^{52} \frac{\partial a_{p,q}}{\partial s_I} \frac{\partial^2 \lambda}{\partial a_{i,(i-12)} \partial a_{p,q}} \right) - \sum_{i=9}^{19} s_{i,(i-1)} \\
 &- s_I \sum_{i=9}^{19} \left(\sum_{p,q=1}^{52} \frac{\partial a_{p,q}}{\partial s_I} \frac{\partial^2 \lambda}{\partial a_{i,(i-1)} \partial a_{p,q}} \right), \\
 \frac{\partial^2 \lambda}{\partial \beta \partial s_M} &= \sum_{i=32}^{43} s_{i,(i-12)} + s_M \sum_{i=32}^{43} \left(\sum_{p,q=1}^{52} \frac{\partial a_{p,q}}{\partial s_M} \frac{\partial^2 \lambda}{\partial a_{i,(i-12)} \partial a_{p,q}} \right) - \sum_{i=21}^{31} s_{i,(i-1)} \\
 &- s_M \sum_{i=21}^{31} \left(\sum_{p,q=1}^{52} \frac{\partial a_{p,q}}{\partial s_M} \frac{\partial^2 \lambda}{\partial a_{i,(i-1)} \partial a_{p,q}} \right), \\
 \frac{\partial^2 \lambda}{\partial \gamma \partial s_P} &= \sum_{i=34}^{42} s_{i,(i+10)} + s_P \sum_{i=34}^{42} \left(\sum_{p,q=1}^{52} \frac{\partial a_{p,q}}{\partial s_P} \frac{\partial^2 \lambda}{\partial a_{i,(i+10)} \partial a_{p,q}} \right) - \sum_{i=23}^{31} s_{i,(i+21)} \\
 &- s_P \sum_{i=23}^{31} \left(\sum_{p,q=1}^{52} \frac{\partial a_{p,q}}{\partial s_P} \frac{\partial^2 \lambda}{\partial a_{i,(i+21)} \partial a_{p,q}} \right),
 \end{aligned}$$

In order to calculate the values of $\frac{\partial^2 \lambda}{\partial a_{i,j} \partial a_{k,l}}$ in the above equations we utilized a method suggested by [34]. In this method matrices Q and its associated group inverse

λ Second order sensitivity	Sensitivity
$\partial\lambda^2/\partial s_I\partial\alpha$	66.2421
$\partial\lambda^2/\partial s_M\partial\beta$	-69.8680
$\partial\lambda^2/\partial s_P\partial\gamma$	-10.8754

Table 3.3: Second-order sensitivities of λ to parameters. The sensitivities are evaluated by using (3.22).

matrix $Q^\#$ are defined as:

$$Q = \lambda I - A \quad (3.20)$$

$$Q^\# = \frac{\bar{y}^t B_{1,1}^{-1} \bar{x}}{y^t x} xy^t + \left(\begin{array}{c|c} B_{1,1}^{-1} - \frac{1}{y^t x} B_{1,1}^{-1} \bar{x} \bar{y}^t - \frac{1}{y^t x} \bar{x} \bar{y}^t B_{1,1}^{-1} & -\frac{y_n}{y^t x} \bar{y}^t B_{1,1}^{-1} \bar{x} \\ \hline -\frac{x_n}{y^t x} \bar{y}^t B_{1,1}^{-1} & 0 \end{array} \right), \quad (3.21)$$

where λ is the Perron value of matrix A , x and y denote corresponding right and left Perron eigenvectors, respectively normalized so that $x^t y = 1$, $B_{1,1}$ the leading principal sub-matrix of order $n - 1$ of Q , and \bar{x} and \bar{y} are the vectors constructed from x and y by deleting their last entries, respectively. Then, in [34][Observation 2.3.4] for second derivatives we have

$$\frac{\partial^2 \lambda}{\partial a_{i,j} \partial a_{k,l}} = x_i y_i q_{j,k}^\# + x_j y_k q_{l,i}^\#. \quad (3.22)$$

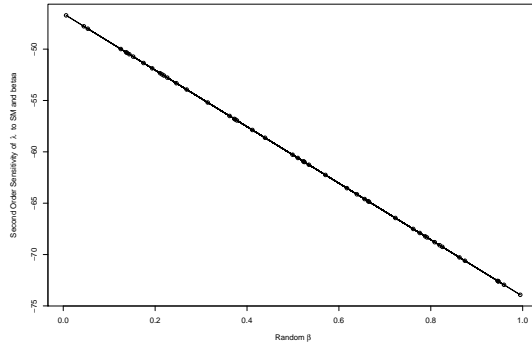
Implementing this formulation with using the estimated parameters (see Table 3.1) we calculate the values of second-order sensitivities.

Values of second-order sensitivities are summarized in Table 3.3. The considerable big values of the second-order sensitivities reveal a high second-order effect of parameter perturbations on the total population growth rate. Moreover, given the fact that all parameters in the model take values in $[0, 1]$, the dependence of first-order sensitivities on parameters values outside of this interval are not so relevant. Thus, in Figure 3.14, we plot the graph of first-order sensitivity functions when parameters are in restricted

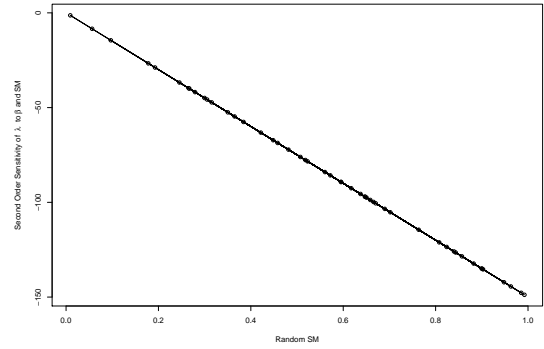
to the interval $[0, 1]$. It is evident that for $\partial\lambda/\partial S_M$, $\partial\lambda/\partial\beta$, $\partial\lambda/\partial S_P$, $\partial\lambda/\partial\gamma$ and $\partial\lambda/\partial S_I$. These sensitivities behave almost similar and are decreasing functions.

Among all second-order sensitivities, $\partial\lambda/\partial\alpha$ is the only one that is an increasing function of immature survival S_I in $[0, 1]$ (see Figure 3.14(e)). Given the negative value of $\partial\lambda/\partial\alpha$ (see Table 3.2), any increase in S_I causes an increase in the absolute value of the effect of α on the growth rate in the long run.

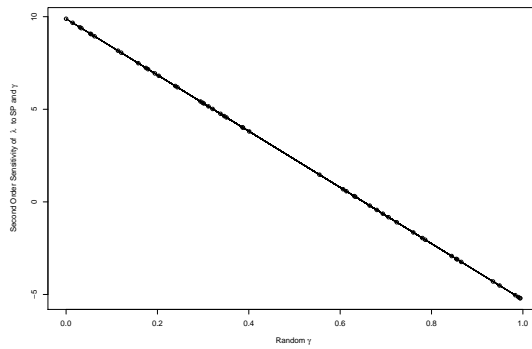
3.5. SENSITIVITY ANALYSIS



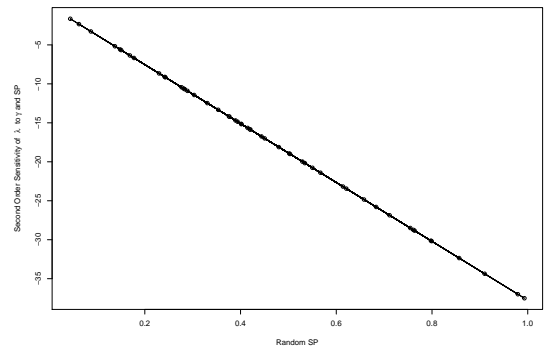
(a) Second-order sensitivity of λ to S_M and β



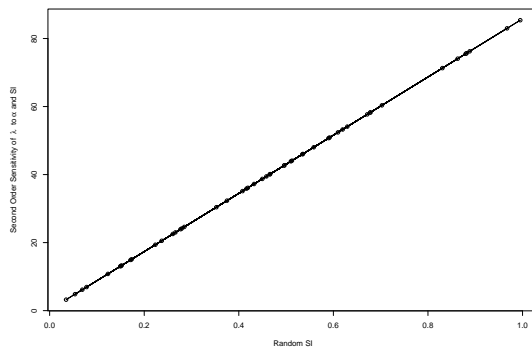
(b) Second-order sensitivity of λ to β and S_M



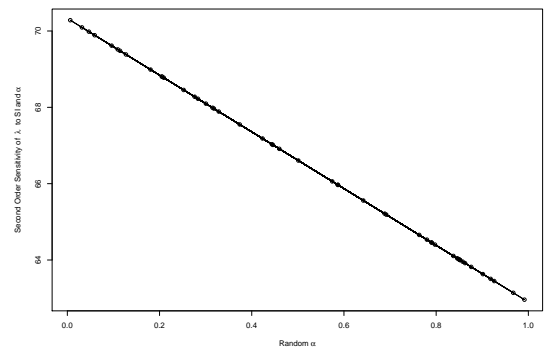
(c) Second-order sensitivity of λ to S_P and γ



(d) Second-order sensitivity of λ to γ and S_P



(e) Second-order sensitivity of λ to α and S_I



(f) Second-order sensitivity of λ to S_I and α

Figure 3.14: Second order sensitivity of λ to model parameters.

Chapter 4

Dynamics of Arctic Charr population in a fluctuating environment

Although the harvesting of wild Arctic populations has been controlled in recent decades and does not seem to represent a serious threat for this species, climate fluctuations, which have accelerated during recent decades, could affect Arctic Charr population vital rates due to their high vulnerability to changes in climate. Sudden changes in climate could be in particular lethal in early ages, when individuals are not yet strong enough to start migration. In this chapter, the effect of varying water temperature on this population is explored. Water temperature is indeed considered a preliminary indicator of climate change in the Arctic and is expected to both rise overall and undergo more pronounced oscillations [29]. In this thesis, data on air temperature is used as a proxy for water temperature, as the later was not readily available.

Two processes are going on simultaneously but on different time scales. The first process is weather change from year to year, which is modelled by a random stochastic process; the second one projects the population from one year to another, with this transition governed by a matrix model as introduced in the previous chapter. Here, we project the population with different transition matrices corresponding to each state of the climate's random process. In other words, in the presence of different climates the population behaves differently and in the following, we investigate the long run behaviour of the population when climate fluctuations are taken into account.

4.1 Transition matrix variations due to climate fluctuations

Three scenarios are considered as the possible situations that the population may face based on climate variations. We define three types of years: good, intermediate and bad. The definitions of these three climate states are based on the effects that experiencing those type of years has on the population growth rate. We use a projection matrix $\tilde{\Pi}_G$ when the population has growth rate greater than one during a good year (the growth rate is assumed to be 1.4). Similarly, we use a projection matrix $\tilde{\Pi}_I$ for an intermediate year, with the rate of growth close to but less than one (the dominant eigenvalue is 0.93). Finally, a matrix $\tilde{\Pi}_B$ projects the population in the presence of a bad climate situation, which results in a rate of growth of 0.53. This indicates a decreasing population growth in the long run.

It is noteworthy that $\tilde{\Pi}_G$, $\tilde{\Pi}_I$ and $\tilde{\Pi}_B$ have the same patterns of non-zero entries as $\tilde{\Pi}$, i.e., :

$$\tilde{\Pi} = \begin{pmatrix} + & 0 & 0 & + & 0 \\ + & + & 0 & 0 & 0 \\ 0 & + & + & 0 & + \\ 0 & 0 & + & 0 & + \\ 0 & 0 & 0 & + & + \end{pmatrix}. \quad (4.1)$$

This common pattern of non-negative entries guarantees common properties for the matrices, such as being irreducible and primitive. Later on, we take advantage of these properties to discuss the limiting behaviour of the population when climate is not constant.

The population projection in four different scenarios is shown in the following figures. Figure 4.1 presents an exponential growth when the population experiences good climate several years in row. Conversely, experiencing several bad years or intermediate years in a row leads to the extinction of the species after just a few years 4.2. Also,

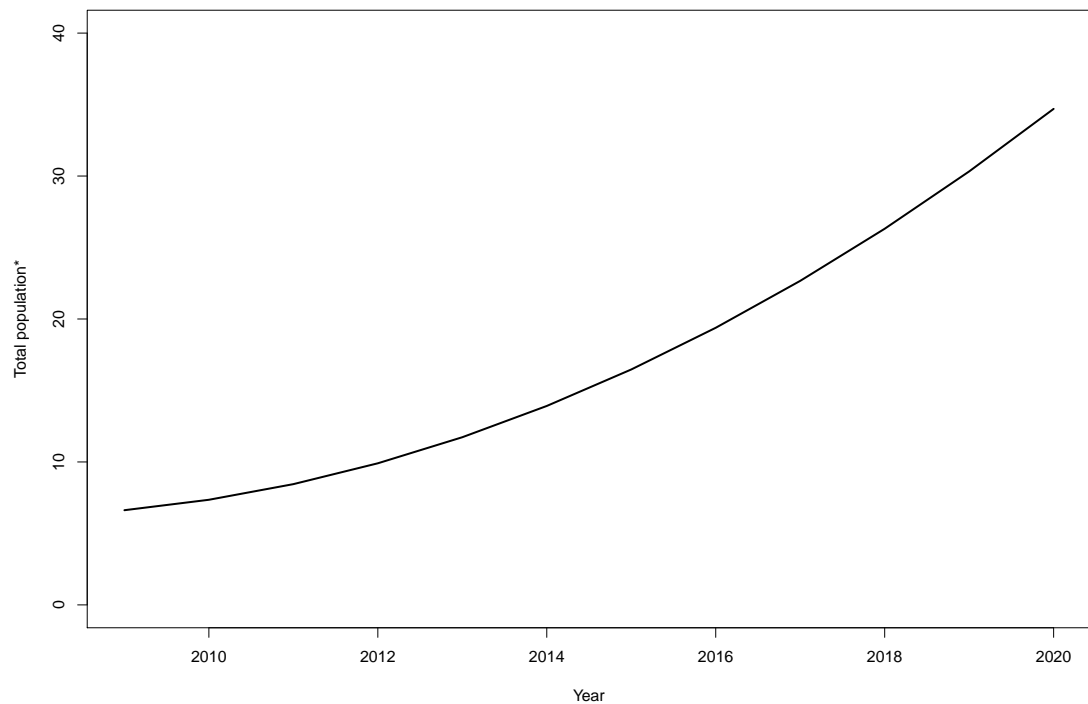


Figure 4.1: Population projection from 2009 to 2020 when a sequence of only good years is assumed to occur. Note that an arbitrary number for total population in 2009 (initial condition) is used. * The population is shown in log scale.

a random transition between the three types of climate (good, intermediate and bad) is considered which, in this case, eventually leads to the extinction of the population, but at a slower pace than the previous cases (see 4.2).

4.1.1 Markov chain transition matrix and climate data

In order to be more precise about the randomness of climate fluctuations, we assume that a stochastic Markov process governs these fluctuations. To do so, we investigate a database (see Figures 4.4 and 4.4) consisting of 39 years of climate data in Cambridge bay, where the demographic data of Arctic Charr were collected. In Figure 4.4, the red straight line is the linear regression fitted to the annual mean temperature curve. This line witnesses a gradual increase in annual mean temperature in Cambridge Bay.

The database includes the mean monthly recorded temperature. Therefore, we consider a discrete time Markov chain with state space the three aforementioned states corresponding to good, intermediate and bad years. In order to form the Markov chain

4.1. TRANSITION MATRIX VARIATIONS DUE TO CLIMATE FLUCTUATIONS

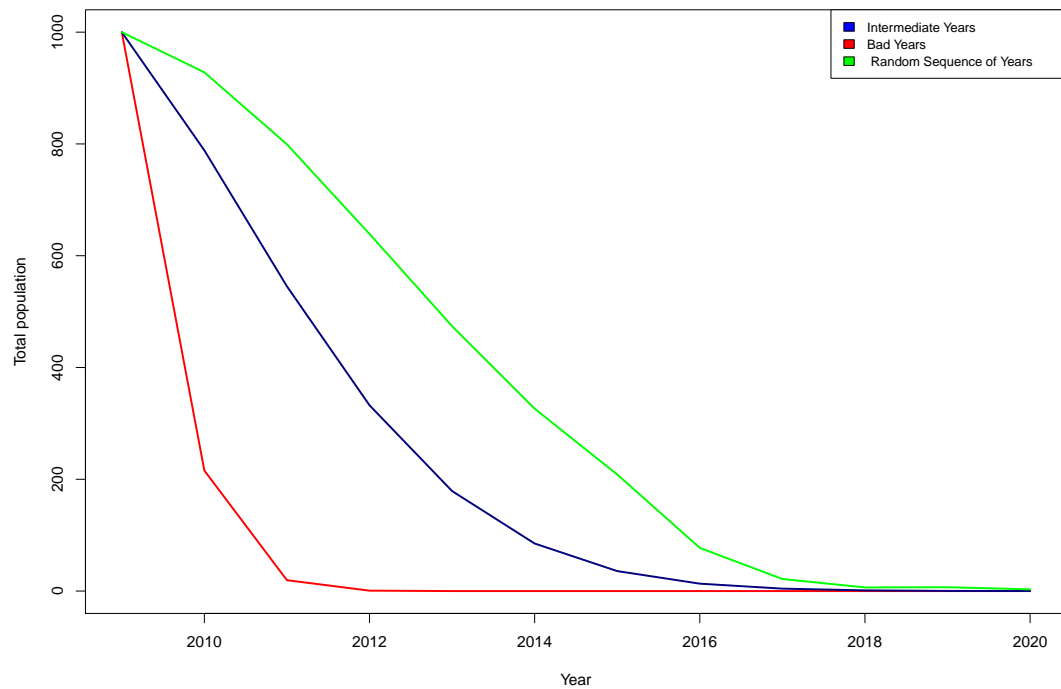


Figure 4.2: Population projection from 2009 to 2020 when a sequence of only bad years (red curve), only intermediate years (blue curve) or a random sequence of good, bad and intermediate years (green curve) is assumed. Note that an arbitrary number for total population in 2009 (initial condition) is used.

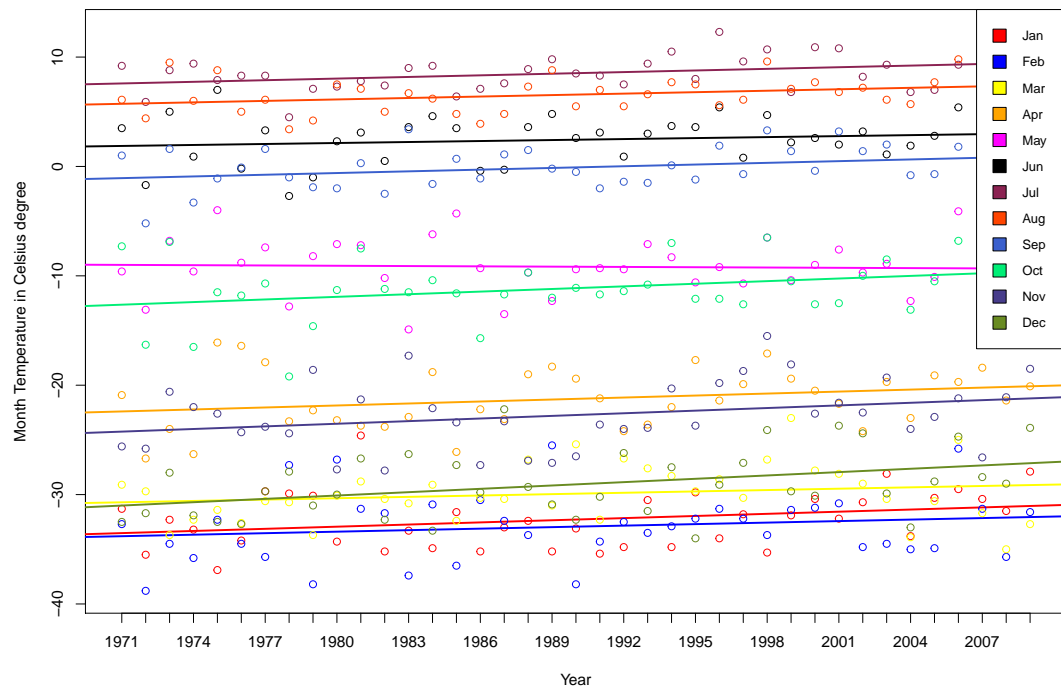


Figure 4.3: Monthly mean temperature in Cambridge Bay, for a period of 39 years and linear fit of these mean temperatures for each month.

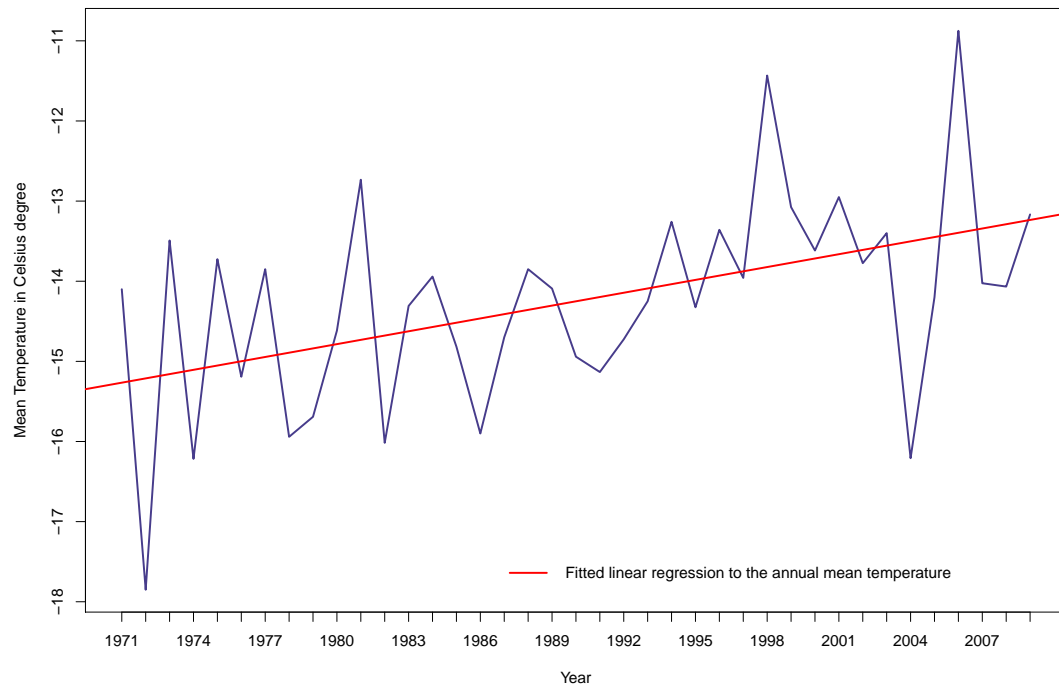


Figure 4.4: Yearly mean temperature in Cambridge Bay, for a 39 years period.

transition matrix, we consider the important events in the Arctic Charr life-cycle (as discussed in Section 3.1.1) to relate the effect of environment on population. Indeed, the sensitivity analysis revealed the high importance of the survival of individuals in the juvenile and immature stages. Thus, we consider the first important events as the reproduction period when the juvenile are born. We also consider the first time migration to sea as the second important event since the immature become mature and experience tremendous environmental changes. Moreover, the optimum thermal thresholds for this species are taken into account. These are summarized below.

Reproduction– spawning

Spawning takes place from late August to late September; water temperature is between $0.5 - 7^{\circ}\text{C}$ in September. Johnson [29] states that water temperature above 5°C a couple of weeks prior to spawning can lead to over-ripe eggs. Therefore, we define a good situation for September months as having water temperature less than 5°C , an intermediate situation is equivalent to temperature $5 - 7^{\circ}\text{C}$; having a temperature

4.1. TRANSITION MATRIX VARIATIONS DUE TO CLIMATE FLUCTUATIONS

above 7°C is considered a bad condition for this month of spawning. In August, as the prior month to the process of spawning, the ideal temperature is assumed to be 5°C and below; the intermediate situation appears in August when the water temperature is between $5 - 10^{\circ}\text{C}$. Above 10°C is assumed to be a bad situation.

Reproduction– incubation

Eggs laid in September hatch late March or early April and the water temperature is about 0.75 to 1.5°C from September to April. The length of incubation¹ decreases for temperature between 4 and 12°C , while egg mortality increases above 7°C and increases extremely at 14°C . Thus, intermediate conditions for the months from October to April are those having water temperature $4 - 7^{\circ}\text{C}$; the ideal situation has temperatures below 4°C ; experiencing mean temperature greater than 7°C can lead to high egg mortality and is interpreted as bad condition for J_0 .

First migration

The first seaward migration, the second important life event for Arctic Charr, happens from mid to late June and ends by mid to late August when the sea water temperature is at most 10°C . The highest growth rate for mature wild Arctic Charr is recorded for the water temperature from $0.5 - 4^{\circ}\text{C}$. Therefore, experiencing water temperature above 15°C can lead to a decrease in mature growth rate while years with June and July temperature from 0.5 to 4°C are assumed to be good years. Summer temperature between 4 to 15°C or below 0°C is considered as an intermediate year. In general, the highest growth rate for the juvenile stage is reported at 13 to 18°C , and mature individuals can tolerate temperature below 18°C , while $20 - 23^{\circ}\text{C}$ can be lethal. Thus, months experiencing water temperatures above $20 - 23^{\circ}\text{C}$ are considered as bad.

We utilized the above mentioned constraints for the important months and, referred to our available temperature database which consists of monthly data for 39 years (from 1971 to 2009). Therefore, we assigned one state of good, intermediate and bad to each

¹Incubation refers to the period that the eggs are laid until they become eyed fish. [4]

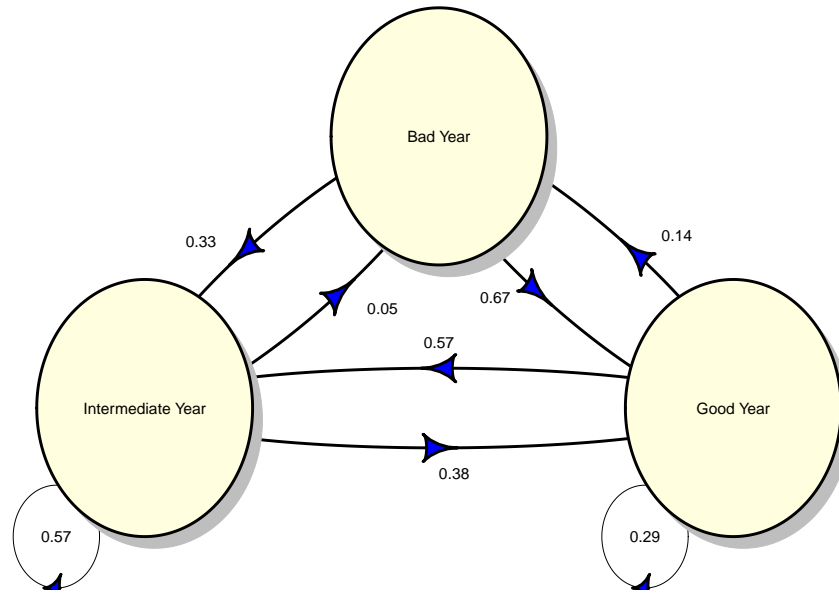


Figure 4.5: Directed graph of the state transitions of Markov chain related to water temperature fluctuations.

month for 39 years data. First, we formed matrix A of size 39×12 which row i th represents the state of 12 different months in year i . In order to form the sequences of states corresponding to each year, we reduce the matrix A to a matrix B of size 39×1 . In fact, we defined the state of each year as the most frequent state in 12 months. For example, for i th year if the “intermediate” state is more frequent than other states in 12 months (consider the i th row of matrix A), then the state of year i is considered as “intermediate”. Using the matrix B as the initial observations of a Markov process we form Markov transition matrix P as follows (see also Figure 4.5).

$$P = \begin{matrix} & \begin{matrix} Bad & Intermediate & Good \end{matrix} \\ \begin{matrix} Bad \\ Intermediate \\ Good \end{matrix} & \begin{pmatrix} 0.00 & 0.33 & 0.67 \\ 0.05 & 0.57 & 0.38 \\ 0.14 & 0.57 & 0.29 \end{pmatrix} \end{matrix}$$

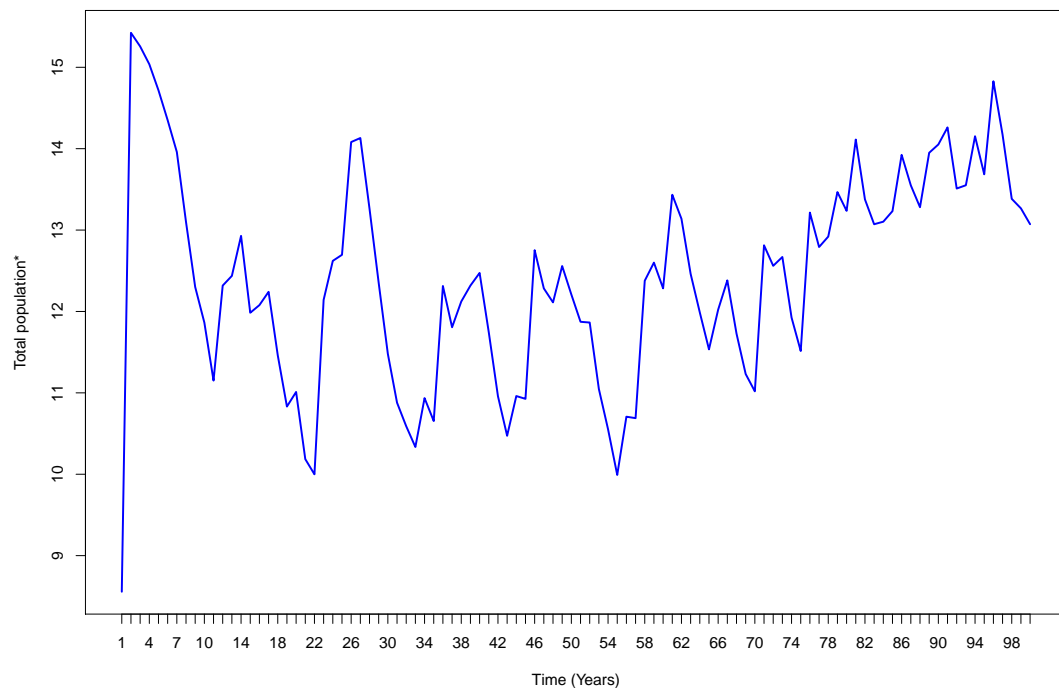


Figure 4.6: Total population projected by the Markov chain over 100 years (* The population is shown in *Log* scale).

4.1.2 Population projection

Having formed the transition matrix of the Markov chain corresponding to changes in temperature, we produce 100 years of climate simulation. Then, we project the population using an initial population vector and matrices $\tilde{\Pi}_G$, $\tilde{\Pi}_I$ and $\tilde{\Pi}_B$. We select the transition matrix depends on climate states that the population experiences in each year. The climate state is equivalent to the Markov chain draws. Figure 4.6 presents the total population during 100 years in the presence of temperature fluctuation for a given sample realisation.

4.2 Stochastic growth rate

As discussed in Section 2.2, it is possible to describe population growth using two indicators:

- The growth rate of the mean population size, $\log E(R)$,

- The time-averaged growth rate over a single realization given, with probability one, as $E(\log R)$.

R_t is the growth rate at time t drawn from a non-negative probability distribution with mean $E(R)$ and variance $V(R)$ in an i.i.d. environment. By the law of large numbers, $E(\log R)$ is the relevant measure of growth rate, at which almost every realization of the process will grow. However, $\log E(R)$ overestimates the growth rate of almost every realization.

Moreover, it is proved not only for i.i.d. process, but also for time-homogenous Markov chains with a primitive transition matrix, that the stochastic growth rate is the most relevant rate [7], which is denoted by $\log \lambda$. This rate can be calculated by (2.43) and two bounds are introduced for this value as in (2.44). Thus, we consider $\log \lambda$ as the growth rate of the population when the environment is fluctuating, since we are considering a time-homogenous Markov chains where the states are drawn from an ergodic set. Also, it is proved in [7] that, eventually,

$$\log \lambda = \lim_{t \rightarrow \infty} \frac{1}{t} \log N(t) \quad (4.2)$$

where $N(t)$ is total population at time t . A maximum likelihood estimator for $\log \lambda$ can be calculated [23] over a large number of simulations T , by

$$\widehat{\log \lambda} = \frac{1}{T} \sum_{t=0}^{T-1} r(t). \quad (4.3)$$

Let $r(t) = \log(N(t+1)/N(t))$, then an approximate 95% confidence interval on $\log \lambda$ is given by

$$\widehat{\log \lambda} \pm 1.96 \sqrt{\frac{V(r)}{T}}. \quad (4.4)$$

Using the estimation method in (4.3), we simulate for 1000 years and the value for

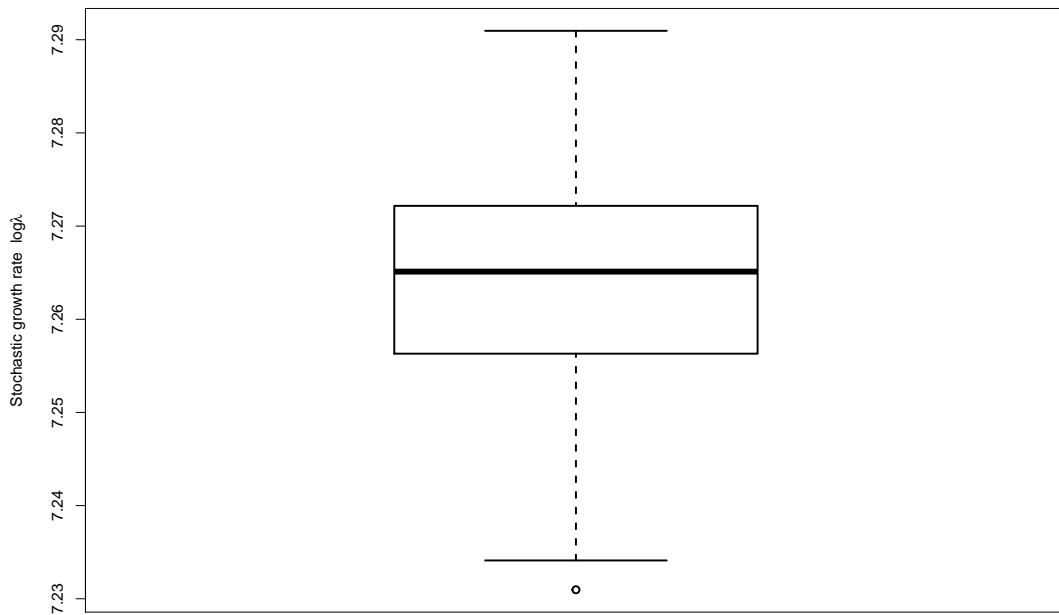


Figure 4.7: Box plot shows the distribution of stochastic growth rate, for 10,000 simulations over 100 years.

$\log \lambda$ is estimated as 7.24 with confidence interval as follows:

$$-6.84 \leq \log \lambda \leq 21.33. \quad (4.5)$$

Thus, for λ we have

$$1.45E - 07 \leq \lambda \leq 2.14E + 21. \quad (4.6)$$

Also, we ran a simulation for 100 different draws of the Markov chain, and the negligible variance of the lower and upper bounds of the confidence interval ($2.47E - 09$) presents the accuracy of the suggested interval. Moreover, different simulations related to the different climate state sequences (but associated to the same Markov chain) have almost the same stochastic growth rate. Figure 4.7 shows small changes in the $\log \lambda$ value for 100 different sequences of climate, each of which is simulated for 1000 years. Next, we examine the influence of initial conditions on the stochastic growth rate. The

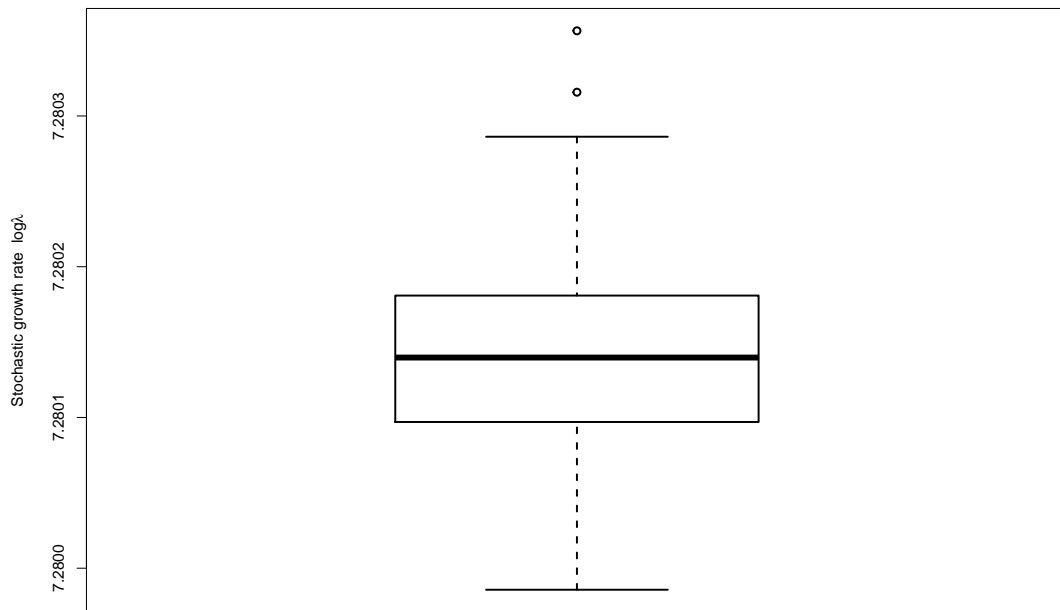


Figure 4.8: Box plot shows the distribution of stochastic growth rate for simulation using 100 different initial age distributions.

results illustrated in Figure 4.8 prove the $\log \lambda$ independence on the initial age distribution. Note that the fertility is considered to be constant and equal to 3500.

As it is discussed in chapter 2 (see 2.56), strictly positive stochastic rate of growth $\log \lambda$ leads to a value less than one for limiting extinction probability $Q_1(\infty)$ as $t \rightarrow \infty$. Thus, having a positive estimate for stochastic growth rate ($\log \lambda = 7.24 > 0$), we expect the population of Arctic Charr survives in the long run.

4.3 Ergodicity

By constructing a 3-state process for climate and then corresponding transition matrices $\tilde{\Pi}_G$, $\tilde{\Pi}_I$ and $\tilde{\Pi}_B$, we project the population using a random sequence of these matrices according to the Markov chain draws. So, we are dealing with a non-homogeneous product of matrices. However, the matrices involved in the matrix product are selected from a fixed set H consisting of the three matrices,

$$H = \{\tilde{\Pi}_G, \tilde{\Pi}_I, \tilde{\Pi}_B\}. \quad (4.7)$$

As discussed, earlier the elements of H share same pattern of non-zero elements and some mutual properties such as irreducibility and primitivity. Having these characteristics guarantees the ergodic behaviour of the population in the weak sense. In fact, based on the definition of an ergodic set in Section 2.6, the set H is an ergodic set. So, any non-homogeneous product of elements in this set is weak ergodic. Thus, as in the constant environment situation, in the long run we expect the population to behave independently of the initial distribution. In other words, two populations with initially different age structures that are subjected to the same sequence of vital rates have age structures gradually becoming similar to each other. As in Section 3.4.2, we consider the limiting behaviour of the population considering four initial conditions to project the population over 100 years. The results exhibit a similar ergodic behaviour and the distribution of age structure becomes independent of initial conditions (see Figure 4.9).

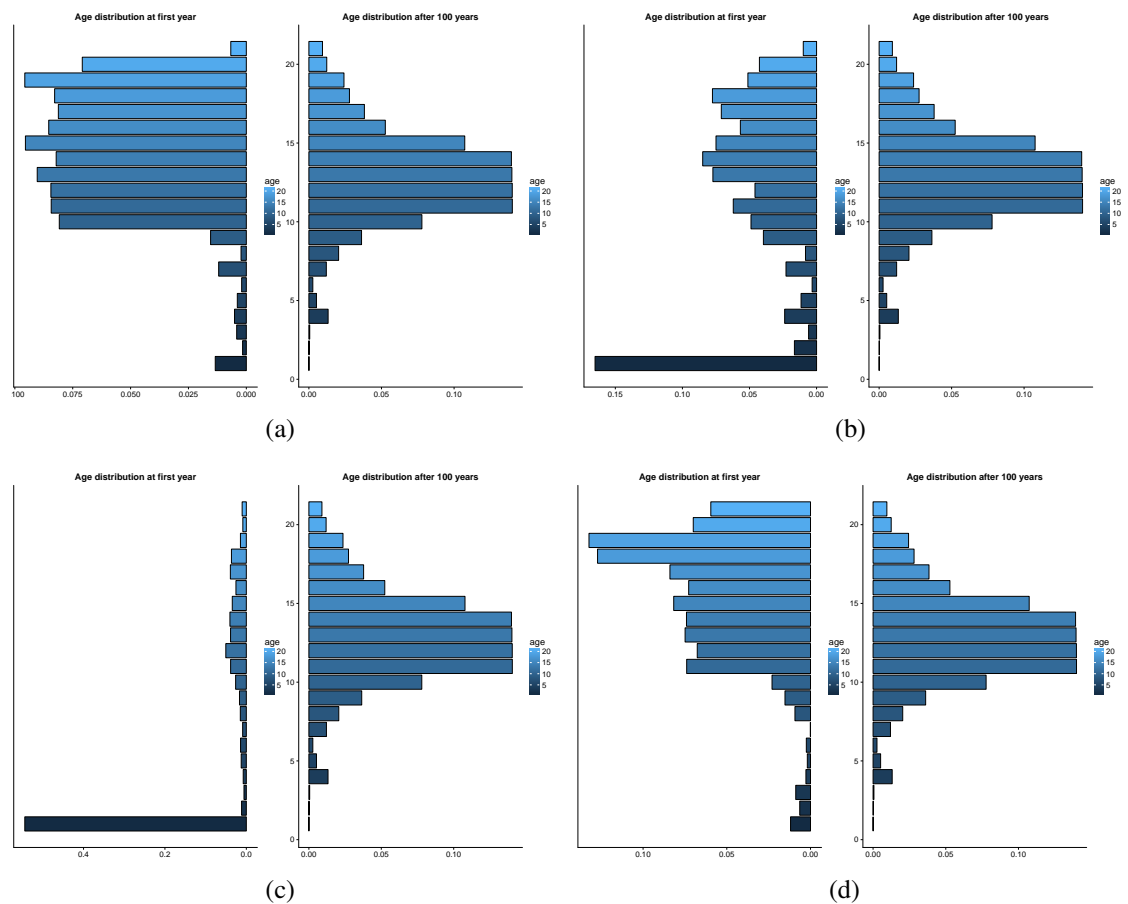


Figure 4.9: Illustration of the consequence of weak ergodicity in a fluctuating environment. Each figure has on the left an initial distribution of individuals in age classes and on the right, the distribution of individuals in age classes after 100 projections (i.e., 100 years).

Chapter 5

Conclusion

In this concluding chapter we summarize the contributions of this thesis and discuss the important directions of future works.

5.1 Summary of thesis contributions

The Arctic Charr population is widely distributed over the Arctic ocean. Current Arctic climate fluctuations and low vulnerability of the Arctic Charr to sudden environmental changes motivate this thesis. Here, we study how experiencing Arctic climate change could affect the dynamics of the Arctic Charr population. We pursue this goal in two steps.

Dynamics of the Arctic Charr population in a constant environment

In Chapter 3, we assume a constant environment and consequently constant vital rates (including survival and fertility). Using a discrete-time matrix formulation we model the transitions of Arctic Charr through its life-cycle. Given the complicated life-cycle of Arctic Charr, the population is clustered based on both age and stage (Figure 3.2). After some simplifications, the transition matrix is non-negative, irreducible and primitive. The first two properties suggest a geometric rate of growth for the population in constant environment; the calculated value for the growth rate suggests to a decreasing population such that extinction is expected eventually. The expectation of eventual

extinction might be a result of the existence or volume of annual harvesting Arctic Charr as well as some underlying assumptions. For instance, we assume a constant environment and the absence of migration. Also, restricted data on the number of young individuals may be another reason for having an unrealistic rate of growth.

To better understand the dynamics of the population in the long run, we study the infinite products of homogeneous chain of matrices. Primitivity of the transition matrix guarantees an ergodic behaviour for the population in the weak sense. Indeed, we show that the population of Arctic Charr forgets its age distributions in the remote past and there is a tendency of population distributions to be proportional (Figures 3.11 and 3.12).

Based on the structure of the available data, a generalized weighted least squares method is utilized to estimate the parameters of the model. The estimated parameters reveal that individuals in the immature stage have the highest survival rate and the individuals in post-reproducing stage have the lowest. The latter might be a consequence of experiencing a high demand reproduction in previous year (Table 3.1). Sensitivity analysis results show a high effect of perturbations in juvenile survivals S_J , on the geometric growth rate λ . Also, it is evident that increasing the transition rate α from immature to mature stage, has negative impacts on λ due to the lower survival in the mature stage comparing to the immature stage (Table 3.2). Significant values of second-order sensitivities revealed high sensitivity of long run growth rate to any perturbation in parameters of the model (Table 3.3).

Dynamics of the Arctic Charr population in changing environment

To describe the problem in the presence of fluctuating environment, in Chapter 4, first it is assumed that the climate changes annually. Then two simultaneous processes are considered. The first process is related to climate change, it is governed by a time-homogeneous three-state Markov chain. The second process projects the population using almost the same model as we described for constant environment, but with different vital rates for each year. The states of the Markov chain are defined corresponding

to three different environmental situations that the population may experience, good, intermediate and bad years (Section 4.1).

A time-homogeneous Markov process with a primitive transition matrix is employed to describe the randomness of the environment. This suggests the stochastic growth rate $\log \lambda$ as the most relevant value for the population growth rate in the long run. In Section 4.2, the stochastic growth rate is estimated as 7.24 in a confidence interval. Evaluating $\log \lambda$ for 1000 years projections using 100 different draws of the Markov chain show the precision of this value (Figure 4.7). Moreover, it is expected that the population of Arctic Charr survives in the long run (probability of extinction less than one) due to the estimated value for stochastic growth rate which is a positive number.

The second process projects the population depending on which state of the environment the population experiences. Therefore, we deal with non-homogeneous products of matrices. Since the participant matrices in the product are drawn from an ergodic set, the behaviour of the population in long term is expected to be ergodic in the weak sense.

5.2 Direction for future work

Theoretical investigation

- This thesis discusses the dynamics of anadromous Arctic Charr. This type of Arctic Charr migrates between sea and fresh water several times over its lifetime. Here, we study the dynamics of the population in the presence of migration between freshwater and sea but in absence of migration between rivers. As a result, the dynamics due to spatial movements are not taken into account. This type of migration might happen if they return to different river after they migrate to sea (30% of migrating individuals migrant to other rivers [29]). Therefore, utilizing a migration model seems interesting and might improve our results.
- In Chapter 4, we formulate transition matrices corresponding to good, intermedi-

ate and bad environmental states ($\tilde{\Pi}_G$, $\tilde{\Pi}_I$ and $\tilde{\Pi}_B$) only based on two main constraints: having similar patterns of non-zero elements as $\tilde{\Pi}$ and having three fixed Perron-Frobenius eigenvalues corresponding to three different types of years. Considering these two constraints, we have many of choices for $\tilde{\Pi}_G$, $\tilde{\Pi}_I$ and $\tilde{\Pi}_B$. Here, we select randomly. Thus, to better understand the dynamics of the population in a fluctuating environment, it would be interesting to improve the definition of those three matrices by using more precise constraints.

- In order to implement perturbation analysis using only sensitivity analysis result can be miss leading since we are estimating fertility as a parameter which takes value in range [1, 4000] while all other parameters of the model are in [0, 1]. Thus, calculating elasticity values can improve our perturbation analysis results.

Database enrichment

Given the high sensitivity of long run growth rate to any perturbations in the parameters of the model, some improvements in database seems to be important.

- From a numerical point of view, we accept some assumptions on the population due to the incomplete data set. For example, a unisex population is assumed because information on the sex of individuals is available only for 7% of total recorded data. Also, only about 52% of data has the age information, so we only consider individuals for which the age is known. We believe that having a database with complete data on sex, age or even stage would significantly improve the accuracy of the results.
- Another aspect of data collection that could be improved is in the area of sampling method. As discussed in Section , individuals of age 5 and younger are not catchable by some methods of sampling (for example gill net). In this thesis, we have to estimate the number of young individuals. This might bring some calculation error to the parameter estimation problem. Also, given the high sensitivity of the growth rate to the dynamics of young individuals (Table 3.2), it is impor-

tant to access a reliable number of individuals in early ages via implementing more appropriate methods of fish catching.

- Here, we used air temperature in Cambridge Bay as a proxy for water temperatures due to our limited access to the relevant data. However, most of the studies discuss the effects of experiencing different water temperature on the Arctic Charr population. Therefore, using real data on water temperature may improve the results in the Chapter 4.

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