



UNIVERSITY OF AGDER

MATHEMATICAL MODEL OF SALMON LIFE CYCLE

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Abstract

Mathematical modeling of the Atlantic salmon population is challenging due to the variability of biological parameters describing its life cycle. Castellani et al. [9] pointed out the scarcity of research on the impact of numerous ecologic and genetic factors on the evolution of populations and emphasized an urgent need for new models incorporating these elements. They suggested an Individual-Based Salmon Eco-genetic Model (IBSEM) describing the demographic and population genetic change of an Atlantic salmon population through its entire life cycle.

The goal of this thesis is to cast biological data available in the research literature into a deterministic stage-structured discrete model described by a system of difference equations accounting for all important stages in the life cycle of Atlantic salmon. Sensitivity and elasticity analyses of the model are conducted along with numerous numerical simulations to provide practical recommendations regarding the impact of the changes to survival rates at different stages on the dynamics of the entire population.

Chapter 1

Introduction

1.1 Motivation

Norway, the world's largest producer of farmed salmon, exported a record 1.2 million tonnes of salmon with a value of NOK 81,269 million in 2021 according to SSB [2], Norway is an essential fish supplier to the world market and this natural resource is necessary for Norwegian economy and the world. Management of the natural resources is required to avoid, for example, overfishing which can lead to depletion of the fish resources, as happened with the Peruvian anchovy stock in the 1970s [11]. Therefore, we need some tools to predict what happens to make those natural resources available for us and the next generations. The prediction is often based on the historical statistical data from fisheries management reporting the quantities given of fish harvested from year to year.

Castellani et al. [9] developed an Individual-Based Atlantic Salmon Population Model (IBSEM) for the Atlantic salmon life cycle, including the processes of growth, mortality, and maturation. The IBSEM model accounts for many variables such as environmental variables and individual genotypes to simulate the demographic and population genetic change of an Atlantic salmon population over its entire life cycle.

When I read this paper and other books and papers about the life cycle of

salmon, I learned how the situation is complicated. This motivated me to attempt the design of a deterministic model of the life cycle of the Atlantic salmon, exploring the possibilities for constructing such models and using them to make meaningful predictions. I intended to write about the salmon's life cycle and how the number of adults in one year influences the number of juveniles and eggs in the following years. I aimed to construct a deterministic model that can estimate the amount of fish in the coming years as well as the optimal harvesting levels (the harvesting levels that do not lead to the extinction of the population in fishery's terminology) by knowing specific factors and using an appropriate model. The right amount of natural resources to be exploited in order for future generations to have access to them. Everything was different with salmon; this type of fish virtually never follows a defined pattern in its life cycle, which means that individual salmon at different life stages can grow, emigrate, spawn, and survive in very diverse ways.

1.2 Research Aims and Objectives

The aim of this thesis is to construct a deterministic model that can predict how the population of the Atlantic salmon changes over time based on the description and the model for the life cycle of salmon in the paper by Castellani et al. [9] and using data from other sources [2, 3, 10].

The objectives of the thesis:

- To review the life cycle of Atlantic salmon following the relevant biological literature and current research.
- Determine the elements that influence the life cycle of the Atlantic salmon.
- Investigate the dynamics of different age classes of the Atlantic salmon and explore the impact of changes in the important biological parameters on the life cycle using sensitivity and elasticity analysis.

1.3 Structure of this thesis

This thesis is organized as follows. In Chapter 1, we provide our motivation for the work, describe the aims and objectives, and explain the organization of the thesis. Chapter 2 introduces and classifies mathematical models. Chapter 3 deals with biological models that study population growth. We described the biology of the salmon and introduced important models that study the salmon population in Chapter 4. Important theoretical results from the theory of non-negative matrices are collected in Chapter 5. Then we introduce our model, study the properties of the population projection matrix, and test it by modifying, in turn, each of the parameters, including the “worst-case scenario.” Furthermore, we conducted full sensitivity and elasticity analyses and summarized our findings. We conclude the thesis with a discussion of the limitations of the model and suggestions for further work in Chapter 6.

Chapter 2

What is a mathematical model?

2.1 Mathematical models

The Dictionary of the public health [30] gives the following definition of the mathematical modeling for biological processes:

A representation of a biological process, system, or relationship by means of a mathematical equation or set of equations, often involving several random variables. The model usually consists of a mixture of variables and one or more associated constants or parameters. A model that does not involve random variables is deterministic. Models can be used to explain complex processes and to predict possible future trends, for instance, in the incidence of diseases.

The purpose of modeling is to provide a tool for understanding what happens in real-world phenomena, including physical, chemical, economic, biological, linguistics phenomena [23], and even in social relations as in the book *The Mathematics of Marriage* [19]. Generally speaking, we can model all complex phenomena around us. We need models to explain and predict processes that

are consistent with what occurs in the real world. We can say that a model is an illustration of what happens in the world, and a good model in most situations predicts what would happen if some parameter changes in the model. The models contain parameters, and the number of parameters rises with the complexity of questions we want to answer with the help of our model. As examples of mathematical modeling in real-life situations, we can mention launching a satellite, flight traffic modeling, highway traffic modeling, and many more.

In his book *Response Surfaces, Mixtures, and Ridge Analyses* [6, p. 424], George Box wrote:

All models are approximations. Essentially, all models are wrong,
but some are useful.

This popular phrase refers to statistical models that are limited and cannot always predict all of the complexities of real-life situations but may be applied to scientific models as well.

2.2 Classification of mathematical models

The simplest mathematical model is, at its most basic level, a functional link between the values of two measurable quantities, one of which we already know and the other about which we desire to learn more. There are many forms of mathematical models; for our need, we can classify, for instance, the mathematical models [29, 31] differently depending on: the subject we study, the purpose of the model, the parameters of the model, the mathematical techniques used to solve the model, the variables in the model, the nature of the model. We present below some popular classifications of mathematical models according to their type.

Linear/Nonlinear In linear models, the rate of change between variables in the model is constant, and we can predict the value of a variable by knowing the value of the other/others. The examples are the equation of a straight line

and linear regression, which describes the relationship between two variables; one of them is dependent on the other. Linear models can be analyzed by dividing them into parts, then solving each one of them, and finally combining the parts to get the answer. This can be done by using techniques such as Fourier analysis, Laplace transforms, or other methods. On the other hand, if the relation between variables is written by a nonlinear equation, then we have a nonlinear model. As an example of a simple nonlinear model, we can write the equation that relates the weight of an individual fish to its length, which can be expressed as follows [12]:

$$W = 8 \cdot 10^{-6} \cdot l^{3.069}$$

where W is the weight of the fish in kg, and l is the fork length in cm (the length of a fish from the tip of its snout to the fork of the tail). These models are more difficult to analyze than the linear models [33], and most of them are impossible to solve analytically since, in the real-life problems, can the parts of the system interact with each other, cooperate or even compete, and the most of the real-life's systems are nonlinear as earthquakes, climate and weather changes, the spread of infections, and many other. Usually, non-linearity is related to phenomena like chaos, even in simple systems.

Static/Dynamic Static mathematical models are usually represented by algebraic equations or functional relations and show us the situations when the system is in the equilibrium state because, in these models, the time is not changing. For example, we may use a static model to compute supply and demand changes in the market model.

The dynamic models are time-dependent, which means that in these models, we calculate the changes that happen in the system with time: We can represent the dynamical models using ordinary, functional, partial differential equations, or difference equations. In differential equations, the time is continuous, but in difference equations, the time, on the contrary, is discrete. Differential equations can also be divided into ordinary where the only variable is time,

and partial differential equations, where the variables are time and space, as in the heat equation.

Discrete/Continuous The mathematical models can be divided into continuous and discrete models, depending on the variable, which is often the time. In continuous models, the variable is a real number $t \in \mathbb{R}$, which means that it could take any number from the set of the real numbers, including the decimals numbers, which means that the changes in the system can occur at any time. While in the discrete models, the variable just takes a natural number, which means that $t \in \mathbb{N}$, which means that the events in the system occur on separate occasions. There are also hybrid models that combine properties of continuous and discrete models. Continuous mathematical models provide us with information about the state of the system at any time and can show us the changes and the effects that occur in the system if we change a parameter.

Descriptive/Predictive Predictive models, as can be deduced from the name, are used to predict the evolution of real systems. I remember in my first year as a master's student; my professor asked me to make a water clock and make an equation that could predict how fast the water would drain from the vessel. That is, by knowing the inputs of our model, the volume of the vessel, and the size of the hole at the bottom, we were able to build a model that makes us capable of predicting the exact time that takes the water to drain from the vessel. Contrary to the predictive models, the descriptive models are used to understand what happened in the past and to understand the nature of a problem or the organization of the system.

There are many different possibilities for classifying mathematical models. In this section, we discussed some possible classifications; a particular model can be classified in many different ways, including various combinations, like nonlinear stochastic models in biology described by stochastic differential equations and simulated numerically or discrete linear models based on difference equations and analyzed analytically. We summarize the classification of mathematical models in the mind map in Figure 2.1.



Figure 2.1: Classification of mathematical models

Deterministic models

I would like to start with one of my favourite quotes [5]

“God does not play dice with the universe.”

This was Einstein’s response to the randomness and probabilistic nature of the quantum mechanic theory. He was dreaming like the rest of us about a predictable world. However, in real-life situations, this is not always the case. As an example, we can mention Heisenberg’s Uncertainty Principle, which states that “We cannot measure precisely the position and momentum of a particle at the same time, and if we in any moment know the position of the particle, we would not be able to measure the momentum of the particle and vice versa”.

When we use a deterministic model, this means that we want to know what happens in the future, and necessarily we should have all the data that make us capable of doing that. In the deterministic models, [37], the present status of the system determines its behavior in the future; we often have most data needed for the prediction model, which makes us capable of making projections for the missing parameters based on the combination of the experimental data and theoretical research. On the opposite, in the stochastic models, the randomness is an essential part, and the variables are usually described statistically by a probability distribution, which implies that the same set of parameters and initial conditions will provide a range of different results.

Chaos

Chaotic behavior may originate in deterministic systems exhibiting irregular behavior that depends on the initial conditions, which in turn leads to unpredictable or random behavior, as in the weather systems. Poincaré was the first person who noticed the possibility of chaos, see [33, p. 3]. In chaotic systems, any small difference in the initial conditions may lead to very different results. However, the physicist Feigenbaum [33, p. 4] discovered in the 1970s that

there are some rules for the transition from predictable to irregular behavior, meaning that different systems can become chaotic in the same way.

2.3 Why do we need models?

- Models supply us with insight into how the system behaves.
- Models can help policymakers make better decisions:
 - By explaining the fundamental causes of complicated phenomena.
 - By predicting what happens in the future.
 - By predicting what happens in response to changes in the system.

In the following list we illustrate where one can make use of the mathematical models:

- Mathematical models are important for studying climate change. Climate sensitivity to changes can be determined with the help of models using simple coupling mechanisms and certain assumptions and conditions or by simulation. Thus, future temperature increases can be predicted.
- Mathematical models help to protect the environment and they are recognized as effective tools for studying the economic and environmental impacts of alternative resources for pollution control - conservation measures - and thus help planners or decision-makers in formulating cost-effective management policies.
- Mathematical models are extremely important in the scientific sciences, particularly physics. Physical theories are basically expressed by mathematics. Molecules, for example, can be represented using molecular orbital models, which are approximate solutions to the Schrödinger equation.
- When engineers analyze a system to be controlled or improved, they often use mathematical models. In analysis, engineers can construct a

descriptive model of the system as a hypothesis of how the system will operate, or attempt to estimate how an unexpected event will affect the system. Similarly, when controlling the system, engineers can try different control methods in simulations.

- Mathematical models contribute to predicting patterns of spread of infectious diseases, and also help to reach community immunity (herd immunity) faster and by using fewer doses of vaccines.
- Mathematical models are increasingly being utilized to investigate inter-group, and national conflicts [17]. The significance of such analysis arises from the fact that empirical studies of disputes are complex and time-consuming. Mathematical models combined with modern computer technology enable the transition from simple fact gathering and analysis to real-time prediction and appraisal of occurrences. Suppose methods of observing and analyzing group conflict allow for a single solution to the conflict event. In that case, mathematical modeling of conflict phenomena using computers allows for the calculation of various options for its development and a prediction of possible outcomes and factors influencing the results.
- Mathematical models simulate complex systems relatively fast and cost less than laboratory experiments. These models describe the essential components of interactions helping to identify methods that are most appropriate and lead to desired outcomes. For medicine, as an example, tumor models can be calibrated using clinical or laboratory data to formulate the hypotheses about tumor behavior.
- Mathematical models are used in biological sciences to understand changing animal populations, the evolution of biological patterns, the spread of disease, and the functioning of the nervous system.

Chapter 3

Biological models of population growth

3.1 Continuous single population models

Population models are constructed on the basis of balance equation:

$$N(t + 1) = N(t) + \text{birth} + \text{immigration} - \text{death} - \text{emigration}$$

where $N(t)$ is the number of individuals at time t and $N(t + 1)$ is the number of individuals at time $t + 1$. In some models, as we will see (Malthus model), for simplicity, we assume that the population is closed, meaning that there is no immigration or emigration, and the birth and death rates are constant.

Malthus model

In his book *An essay on the principle of population* published in (1798) [27, p. 5], Malthus wrote:

“I say that the power of population is indefinitely greater than the power in the earth to produce subsistence for man. Population, when unchecked, increases in a geometrical ratio. Subsistence increases only in an arithmetical ratio. A slight acquaintance with

numbers will shew the immensity of the first power in comparison of the second.”

He predicted that the population number would expand exponentially, and this would lead to disasters because the food supply could not reasonably be grown at a continual positive per capita growth rate to keep up with the population expansion. The Malthusian model is the simplest growth model of a single population, which assumes that “The population is homogeneous and isolated, and the habitat is invariant.” The main reasons for changing population size are death, birth, emigration, and immigration, but in the Malthusian model, we assume that the population is closed, then the population change is just by birth and death. For describing the Malthus growth equation (model), we follow the explanation from the books [7, 22], and this can be done as follows. We assume that the density of the population at the time (t) is denoted by $X(t)$ and let $X(t)$ be continuous and differentiable everywhere. In some populations, there is a proportional relation between the number of new members and the number of members at present during a short time interval of the length Δt , each individual gives birth to $\beta\Delta t$ new individuals, and in the same period, each individual has probability $\mu\Delta t$ of dying, where β, μ denote the per capita birth rate and per capita death rate, respectively. During this period Δt , the total population gives birth to $\beta\Delta tX(t)$ and the death in the total population is $\mu\Delta tX(t)$. In a short time we have

$$N(t + \Delta t) - X(t) \approx \beta X(t)\Delta t - \mu X(t)\Delta t \approx (\beta - \mu)X(t)\Delta t.$$

Dividing both sides by Δt , we obtain:

$$\frac{X(t + \Delta t) - X(t)}{\Delta t} \approx (\beta - \mu)X(t).$$

Passing to the limit as $\Delta t \rightarrow 0$, we have

$$\lim_{\Delta t \rightarrow 0} \frac{X(t + \Delta t) - X(t)}{\Delta t} = (\beta - \mu)X(t).$$

This can be written in the form of a differential equation

$$\frac{dX(t)}{dt} = (\beta - \mu)X(t).$$

Denoting $\beta - \mu = r$ we introduce r , the instantaneous growth rate. The solution of the differential equation

$$\frac{dX(t)}{dt} = rX(t) \tag{3.1}$$

with the initial condition $X(0) = X_0$, is given by $X(t) = X_0e^{rt}$. This is why we call Malthus model the exponential growth model. We have three alternatives: (i) if $r < 0$, the population will go extinct; (ii) if $r > 0$, the population will grow; and (iii) the population size does not change if $r = 0$. We can see in Figure 3.1 how the exponential growth changes with different value of the growth rate.

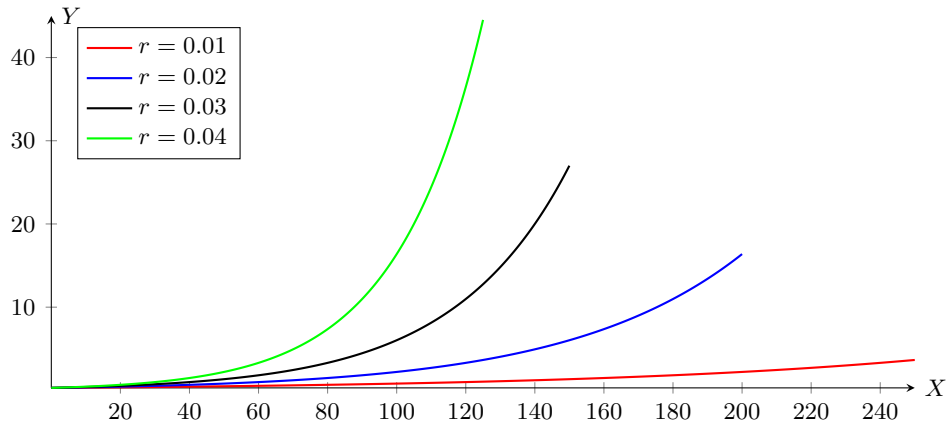


Figure 3.1: Malthusian growth for different positive values of r .

It is clear that Malthus's model is unrealistic and is very simple because there are many factors affecting population growth besides death and birth, such as immigration and emigration. The next step in the development of the population models is the logistic model.

Verhulst model

This model is also known as the logistic model. In this model, the habitat is assumed to be limited so that it can not support the growth if the population reaches a certain level called the carrying capacity (the maximum sustainable population). After this, fertility will decrease, and mortality will increase. We can write the differential equation as

$$\frac{dX(t)}{dt} = rX \left(1 - \frac{X}{K} \right). \quad (3.2)$$

It follows from the analysis of the right-hand side of equation (3.2) that

$$\begin{cases} X > K & \Rightarrow & \frac{dX}{dt} < 0 & \text{and} & X & \text{decreases;} \\ X < K & \Rightarrow & \frac{dX}{dt} > 0 & \text{and} & X & \text{increases.} \end{cases} \quad (3.3)$$

The solution of equation (3.2) is given by

$$X(t) = \frac{KX_0}{X_0 + (K - X_0)e^{-rt}}, \quad (3.4)$$

but its behaviour is already explained by (3.3). We plotted solutions to the logistic equation for different values of the carrying capacity in Figure 3.2.

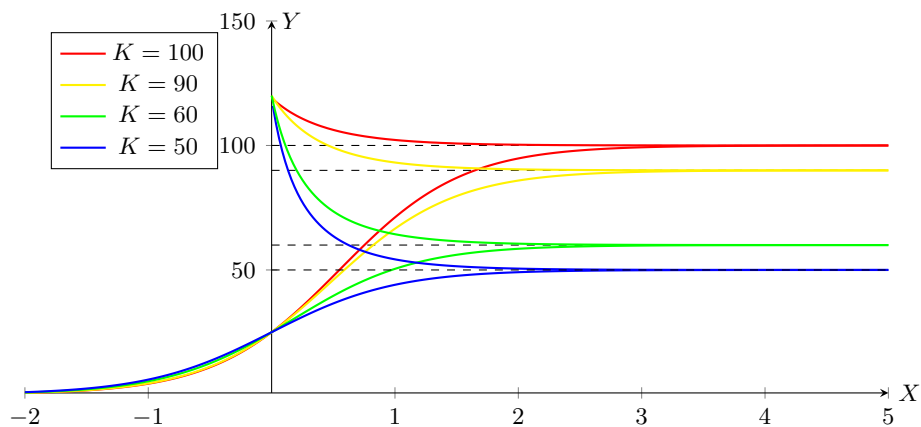


Figure 3.2: Verhulst model for different carrying capacities $K = 100, 90, 60, 50$, $r = 2$, and initial conditions $X_0^1 = 120, X_0^2 = 25$.

Schaefer model

Schaefer's model is based on the logistic growth model, but it also incorporates harvesting. It can be written in the form:

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{K}\right) - qXE \quad (3.5)$$

where X is the biomass, K is the carrying capacity, i.e., the maximum population size that can be achieved in the habitat, and r is the intrinsic growth rate of the population. The difference with equation (3.2) is that (3.5) includes the harvest H introduced as

$$H = qXE \quad (3.6)$$

where q is the catchability coefficient defined as the fraction of the biomass caught by the unit of fishing effort [8], and E is the fishing effort representing the amount of fishing gear of a specific type used on the fishing grounds over a given unit of time, e.g., hours trawled per day, the number of hooks set per day, or the number of hauls of a beach seine per day [1]. Generally, fishing efforts are regulated by quotas, trip limits, and gear restrictions. From equation (3.6), we can see that the harvest per unit effort is a function of the size of the population, $H/E = qX$. The Schaefer model uses the following assumptions [28, p. 167]: different species do not interact with each other; r is independent of age composition. the environmental factors do not affect the population; there is no time delay in the response of r to the change in the biomass (X); q is constant; the death for a natural reason and the death due to fishing happen at the same time; the efficiency of the vessels does not change; the statistics on the effort and the catch are correct.

3.2 Continuous multi-species models

Predator-Prey models

Lotka-Volterra

Lotka-Volterra equations, also known as the predator-prey equations [7], is presented as a system of first-order nonlinear differential equations. They are used to explain the dynamics of biological systems involving two species, one of which is a predator and the other is prey. We denote by x the number of prey and by y the number of predators. In this model, we have three assumptions: (i) The food supply of the prey is unlimited, and if there is no predator, the population of prey will grow exponentially,

$$\frac{dx}{dt} = \lambda x, \quad (3.7)$$

where λ is the growth rate of the prey.

(ii) The predator depends on the prey as food, and in the absence of the prey predator population decays exponentially,

$$\frac{dy}{dt} = -\mu y, \quad (3.8)$$

(iii) If the predator hunts the prey, then the number of predators will increase from $-\mu$ to $-\mu + cx$, with the rate c and the number of the prey will change from λ to $\lambda - by$ where b is the coefficient that determines the rate of predation, i.e., the probability of the predator catching the prey.

Then Lotka-Volterra equations are written in the form:

$$\begin{aligned} \frac{dx}{dt} &= x(\lambda - by), \\ \frac{dy}{dt} &= y(cx - \mu). \end{aligned} \quad (3.9)$$

3.3 Age-structured discrete models

The word "*structured*" means that the model is organized according to a pattern; the most obvious pattern to recognize the difference between the individuals in a population is the age or size. The age of individuals affects the birth and death rates of the population. To account for the impact of age, we must represent the population by variables $N_i(t)$ that represents the number of individuals of age i at time t , with i that range between 0 to the maximum age of the individual.

Leslie Model

The Leslie model [26, 36] is an age-structured single-species population growth model. In the Leslie model, we only consider the female population, assuming that males would always fertilize females. Females are classified into age groups by equal time units. The time unit $(1, 2, \dots, m)$ might be a second, a day, a month, a year, or something else. For humans, for example, we use a 5-year time unit, whereas, for whales, we use a 2-year time unit [35]. In the Leslie model, the fecundity and survival rates do not change with time; therefore, they are independent of the population density. The life table shows the probability of death of an individual at a specific age. In other words, it demonstrates the population's ability to survive. The life table may also be given as a long-term mathematical approach to calculating population lifespan. To construct the Leslie matrix, we need to define some important notions and notation. In what follows, l_i is the number of individuals surviving to the age i , it is given by the equation

$$l_i = \frac{N_i}{N_0},$$

where N_0 is the number of individuals at birth, and N_i is the number of individuals at age i . The survival probability p_i is the probability that an

individual in the i -th age group will survive to join the $i + 1$ -st age group,

$$p_i = \frac{N_{i+1}}{N_i} = \frac{N_{i+1}/N_0}{N_i/N_0} = \frac{l_{i+1}}{l_i}.$$

Per capita fertility rate f_i is the mean number of offspring an individual can have in the i -th age group.

Furthermore, Σf_i is the gross reproduction rate, defined as the total number of daughters born for the total population in the absence of mortality, and $R_0 = \Sigma f_i l_i$ is the replacement rate (or net reproductive rate), the total number of daughters born for the total population, taking into account the mortality. The net reproductive rate is a useful indicator of population fitness. If $R_0 > 1$, the population size will increase; if $R_0 = 1$, the population size will remain at the same level, and if $R_0 < 1$, the population size will decrease.

Other useful characteristics are the generation time $T = \frac{\Sigma i \cdot l_i \cdot f_i}{R_0}$, the average period between the birth of an individual and the birth of its offspring, and the intrinsic growth rate $r \approx \frac{\log(R_0)}{T}$.

One has to distinguish between the post- and pre-breeding models, depending on when the births occur in relation to the annual census. To understand this, assume that we run a census every January 1st. In some populations, such as humans, which give birth to new individuals throughout the year, we count the offspring F_i the average number of births to individuals in age i whose offspring survive the same date of the next year. In other populations, the birth happens once a year, often at a specific season, so we count the offspring as the number of individuals. So when the offspring happens in a specific season, we count the number of individuals after birth. If we have f_i is the number of the offspring that each individual at age i has at the present birth pulse, then the census of the current population after the pulse can be calculated by the equation $F_i = p_i \times f_{i+1}$ where p_i is the survival probability to the next year and f_{i+1} is the number of the offspring in the next year's pulse. This is what we call a post-breeding census.

On the other hand, if we count the population's number before the pulse, then

we will have the pre-breeding census $F_i = p_0 \times f_i$ where p_0 is the probability that offspring survive, and f_i is the number of the offspring now which will be counted the next year.

Both ways of counting the population size are valid with appropriate assumptions. In the Leslie model, we assume that the probability of survival of the last age group is zero, that is, $p_m = 0$. Let $N_i(t)$ be the population size of the i -th age class at the time t . We can make two assumptions:

(1) The individuals in the group i at time t enter age $i + 1$ at time $t + 1$ with the survival probability p_i for the i -th age group. Thus

$$\begin{aligned} N_2(t + 1) &= p_1 \cdot N_1(t); \\ N_3(t + 1) &= p_2 \cdot N_2(t); \\ &\vdots \\ N_m(t + 1) &= p_{m-1} \cdot N_{m-1}(t). \end{aligned}$$

(2) During time period t , each individual in age group i has on average f_i offspring. Thus individuals in age group i produce $f_i \cdot N_i(t)$ female offspring during time period t which enter the first age-class at time $t + 1$:

$$N_1(t + 1) = f_1 \cdot N_1(t) + f_2 \cdot N_2(t) + \cdots + f_m \cdot N_m(t).$$

Using our assumptions, we can write

$$\begin{aligned} N_1(t + 1) &= f_1 \cdot N_1(t) + f_2 \cdot N_2(t) + \cdots + f_m \cdot N_m(t), \\ N_2(t + 1) &= p_1 \cdot N_1(t), \\ N_3(t + 1) &= p_2 \cdot N_2(t), \\ &\vdots \\ N_m(t + 1) &= p_{m-1} \cdot N_{m-1}(t). \end{aligned}$$

We can write these equations in the matrix form

$$\begin{pmatrix} N_1 \\ \vdots \\ N_m \end{pmatrix} (t+1) = \begin{pmatrix} f_1 & f_2 & \cdots & f_m \\ p_1 & 0 & \cdots & 0 \\ 0 & p_2 & \cdots & 0 \\ \vdots & & \ddots & \\ 0 & \cdots & p_{m-1} & 0 \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \\ \vdots \\ N_m \end{pmatrix} (t)$$

$$N(t+1) = AN(t) \tag{3.10}$$

where the vector

$$N(t+1) = \left[N_1(t+1), N_2(t+1), \dots, N_m(t+1) \right]^T$$

represents the population at time $t+1$, and

$$N(t) = \left[N_1(t), N_2(t), \dots, N_m(t) \right]^T$$

represents the population at time t .

The square matrix A with non-negative entries where all entries are zeros except for the first row and the sub-main-diagonal,

$$A = \begin{pmatrix} f_1 & f_2 & \cdots & f_m \\ p_1 & 0 & \cdots & 0 \\ 0 & p_2 & \cdots & 0 \\ \vdots & & \ddots & \\ 0 & \cdots & p_{m-1} & 0 \end{pmatrix}$$

is called the Leslie matrix. Applying equation (3.10) k times, we obtain

$$N(t+k) = A^k N(t). \tag{3.11}$$

Since the matrix A is a square matrix with m rows and columns, there will be

m latent roots and vectors which satisfy the equation:

$$AN = \lambda N \tag{3.12}$$

where λ is a latent root (latent roots are solutions of the characteristic equation for the square matrix A [20]) and N is a latent vector associated with λ . The Leslie matrix is a useful tool to explore the population growth for closed cohorts. It does not account for migration and uses only the number of females. However, as we will see later in Chapter 5, the Leslie matrix does not provide a good description for animal cohorts where the age of the individuals is less important because some individuals can grow faster than others. Twins may show a huge difference in development in size, which leads us to the next step, the Lefkovich model.

Stage structured discrete models

Lefkovich model

In some animal populations, it is impossible to determine the actual age of the individuals [25]. Therefore, the Lefkovich model [34] does not take into account the age but instead divides the population using their development stages which can easily be recognized by the size of the animals. The Lefkovich transition matrix shows the transitions between the different stages and is used to represent the stage-structured model. In the stage-structured models, the number of individuals in the population at the time $t + 1$ depends on the number of individuals at each stage at the time t , besides the transition from and to stages and the mortality of individuals. Thus, in the stage-structured models, we have three options: the individual remains at the same stage, grows up to the next stage, or dies. Here, we assume that $N_i(t)$ represents the number of animals at the stage i at time period t . Let b_i ($i = 0, 1, 2, \dots, m - 1$) be the probability that an individual moves from the stage i to the stage $i + 1$, and a_i ($i = 0, 1, 2, \dots, m$) be the probability that an individual remains at

the same stage. Then we have

$$a_i + b_i = 1 \quad (i = 0, 1, 2, \dots, m - 1),$$

with the following bounds on the probabilities $0 \leq a_i < 1$ and $0 < b_i \leq 1$. If $a_i = 1$, then $i = m$, since we would not have a transition from the last stage. Then we have the following system of equations for the number of individuals at each stage:

$$\begin{aligned} N_2(t+1) &= b_1 \cdot N_1(t) + a_2 \cdot N_2(t), \\ N_3(t+1) &= b_2 \cdot N_2(t) + a_3 \cdot N_3(t), \\ &\vdots \\ N_m(t+1) &= b_{m-1} \cdot N_{m-1} + a_m \cdot N_m(t). \end{aligned}$$

As in the Leslie model, during time t , each individual in the age group i has on average f_i offspring. Thus, the individuals in age group i at time t produce $f_i \cdot N_i(t)$ female offspring which enter the first age-class at time $t + 1$:

$$N_1(t+1) = f_1 \cdot N_1(t) + f_2 \cdot N_2(t) + \dots + f_m \cdot N_m(t).$$

Then the recruitment data can be presented by the matrix:

$$B = \begin{pmatrix} f_1 & f_2 & f_3 & f_4 & f_5 & \cdots & f_m \\ b_1 & a_2 & 0 & 0 & 0 & \cdots & 0 \\ 0 & b_2 & a_3 & 0 & 0 & \cdots & 0 \\ 0 & 0 & b_3 & a_4 & 0 & \cdots & 0 \\ 0 & 0 & 0 & b_4 & a_5 & \cdots & 0 \\ & & & & \ddots & & \\ 0 & 0 & 0 & 0 & 0 & a_{m-1} & 0 \\ 0 & \cdots & \cdot & \cdot & \cdot & b_{m-1} & a_m \end{pmatrix}.$$

Given the column vector $N(t) = \left[N_1(t), N_2(t), \dots, N_m(t) \right]^T$ which represents the numbers of the animals at time t , and, similarly, if the vector $N(t+1)$ representing the number of animals at time $t+1$, we can write that

$$N(t+1) = BN(t). \tag{3.13}$$

We can study quantitative changes in the natural resource by comparing the population structures at periods t and $t+1$. If we have stable age distribution then the number of animals at time t must be proportional to the number of animals at time $t+1$ for each class,

$$N(t+1) = \lambda N(t).$$

and we get from the equation (3.13) that

$$BN(t) = \lambda N(t).$$

This means that λ is a latent root of the matrix B . If $\lambda > 1$, we will have an increase in the number of animals over time, and the increasing value is a measure of the potential harvesting.

Chapter 4

Biological factors affecting salmon live cycle

4.1 What are the challenges with salmon?

It is a highly complex life, that of salmon. The salmon are born in freshwater and live there as juveniles until they grow to a certain size, which makes them able to survive in the saltwater, then travel to the ocean to grow more and become adults. After that, they come back to the freshwater to reproduce. Some juveniles (male parr) can reproduce although they may be eaten or attacked by the adults; therefore, they sneak into the spawning among the adults. Moreover, some juveniles may grow in the first year and immigrate to the ocean, but on the other hand, some juveniles can remain at the same stage for up to seven years. Some adults spend one year in the ocean, and some may stay up to seven years before they come back to spawn. Some adults die after spawning, and some may spawn several times. These differences in the life patterns of individual salmon may be beneficial because they make salmon flexible to the changes.

The Atlantic salmon population faces many challenges, including predators, pollution, climate change, harvesting, and human-made changes to the natural habitat, such as making dams on the rivers where Atlantic salmon live or

migrate.

4.2 The life cycle of the Atlantic salmon

In this section, we provide a brief description of the life cycle of salmon following that in the book *Atlantic Salmon Ecology* [3, p. 4-6]. Atlantic salmon live in the arctic and subarctic zones. The species has a wide range of complex life cycles. However, most of them are anadromous, which means that they hatch and live as juveniles in the same area in freshwater, then travel to saltwater to grow up. When they become adults, they come back to the same spawning sites to reproduce. We can summarize the life cycle of the Atlantic Salmon in steps as follows.

- From September through February, Atlantic salmon spawn in rivers.
- In the following spring, the eggs hatch, and the tiny fish are known as alevin (15-25 mm). They live on their yolk sac for 3 to 8 weeks until emerging from the gravel and becoming fry, at which point they start feeding in freshwater.
- Juvenile (parr) can be in the freshwater for one to eight years before they transform into smolt (10-20 cm) that travel to the ocean, and after they enter into the saltwater, they are called post-smolt.
- Through their life at sea, the salmon grow in weight from 50 g to 1-25 kg before returning to spawn.
- A large number of salmon die after the spawning season due to illnesses, exhaustion, and predators.
- Individuals can spawn up to seven times throughout their lifetime. However, the majority only spawn once or twice.

- Before they emerge to the sea, some of the parr may reach sexual maturity and be able to produce viable sperm. Still, the adult females are not interested in them, so they do not exhibit courting, and instead, they sneak spawn near pairs of adult fish.

4.3 A one-year life cycle of the Atlantic salmon

Based on the IBSEM model [9], we summarize the main events in the life of the Atlantic salmon in one year.

- October 1, spawning, laying eggs.
- November 1, to March 1, resting season where the fish does not grow up.
- November 1, to May 1, the transition from parr to smolt.
- April 1, hatching eggs.
- May 1, the transition from alevin to parr.
- May 1, to November 1, growth season.
- May 1, the transition from smolt to adult.
- the adult and smolt do not have a resting season. i.e., they grow all year round.

Figure 4.1 summarizes the life cycle of salmon during one year.

4.4 Mathematical models of salmon life cycle

There are too many difficulties in determining how a population will react to the changes in the environment [32]. One technique that helps us deal with these issues is to understand the features of individuals, analyze how the environment influences changes in these elements, and then develop a structure of population dynamics. There are several methods to do so, including matrix

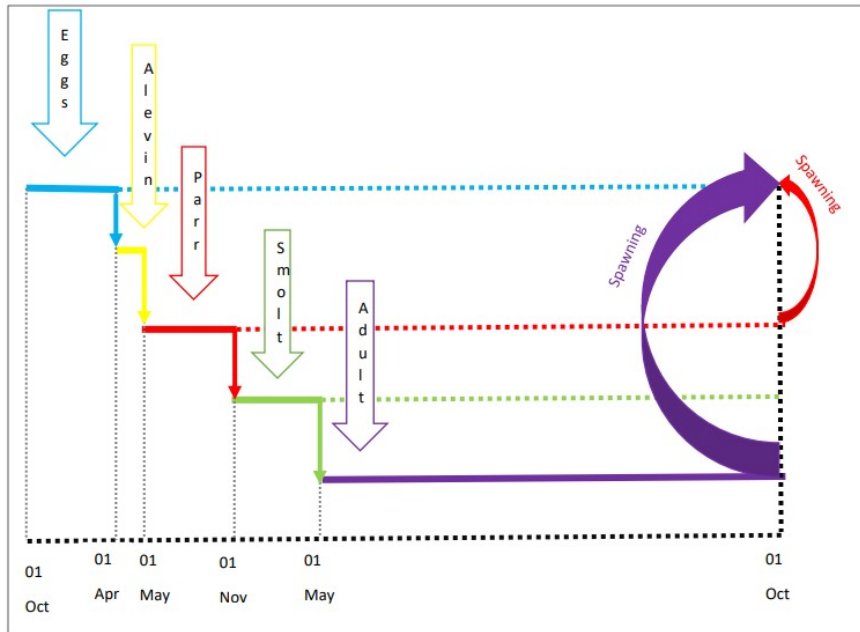


Figure 4.1: The life-cycle of the salmon during one year

population models, delay differential equation models, individual-based models, and integral projection models. There are two types of mechanistic population dynamics models: group-based models, in which the population is divided into size or age groups, and individual-based models, which describe the interactions between individuals based on the characteristics of each individual in the population. In the individual-based models for salmon fish [21], we model the growth rates, the migration, the predator-prey interactions, and genetic elements, besides many other environmental elements. We present two useful models.

IBSEM model

There are several studies that consider the ecology and genetics of the Atlantic salmon. The IBSEM model (Individual-Based Salmon Eco-genetic Model) is one of such models. Castellani et al. [9] designed a model that considers the ecology and genetics of the individuals Atlantic salmon as well as the

environmental variables. They simulated growth, mortality, and maturation through stochastic procedures, and the result of the simulations showed that the model reproduces the characteristics of the population, and this is due to the mix which happens to the salmon population with non-local populations. The differences in the origin of the fish can be divided into wild, farmed, or hybrid, which can be seen in the genotype of the individuals. These differences influence the growth, survival, and maturation of individuals. In IBSEM model the life cycle of the salmon is divided into three stages: embryonic, juvenile, and adult. The embryonic stage in freshwater is divided into two stages: egg and alevin. Juvenile stage is divided into parr and pre-smolt stages. Eggs hatch in April, and on the first of May, the alevin enters the parr stage and begins to feed in the river. Parr has been divided into stages based on its age: (+0) Parr with age less than one year, (+1) one-year-old parr, and (+2) parr older than two years. The transition from parr to smolt is variable and can vary between one year to several years. The probability of this transition depends on the size of the individual. The year is divided into resting seasons when parr does not grow up in the cold months (November-February) and the growth seasons when parr is growing up in the warm months (March-October). There is a possibility of a male parr to mature sexually in October and engage in the reproducing process known as sneak spawning. The smolts grow in the resting seasons, remain six months in the sub-phase, and migrate on the first of May to the ocean as adults. The adults may stay in the ocean up to three years, and they return to spawn in October, and the returning probability is depending on the age and genotype of the individuals. There is a percentage of adults that survive after spawning (they are known as kelts) and travel once again to the ocean. The adults are grouped depending on the years spent at sea into: (0SW) as the first year at sea, (1SW) one year, (2SW) two years, and (3SW) three years or more at sea. Figure 4.2 illustrates the life cycle of salmon according to the IBSEM model. Castellani et al. [9] introduced the IBSEM model to explain the life cycle of a wild salmon population that inhabits in

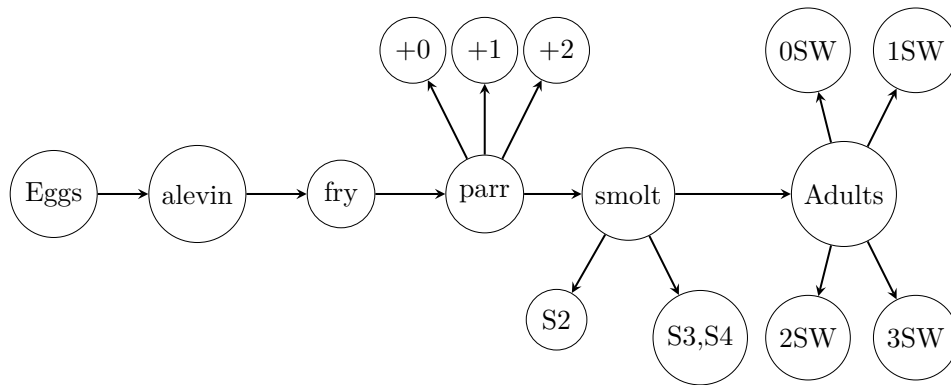


Figure 4.2: The life cycle of salmon according to IBSEM

the river Os in Norway and migrates to the Norwegian Sea during its oceanic phase.

A model of the complete life-cycle of Atlantic salmon based on spatially explicit individual-based approach

Hedger et al. [21] developed a model that predicted the whole life cycle of the salmon in the freshwater by using the individual-based mechanistic approach. They used a hybrid model that includes both a deterministic part that can predict the processes that affect the abundance of the salmon in different stages, and the stochastic part used to calculate the probability of birth, death, smolting, and returning of the adult fish to the freshwater. The model includes the following factors: the time of year when spawning occurs, the section of the river where spawning occurs, the river/sea where the salmon lives, body mass and length, variance in growth among individuals, the developmental stages of the salmon, age in weeks, the age of the cohort, and the number of winters spent at sea. The functions in this model were picked from the literature or developed via actual research at the Norwegian Institute for Nature Research (NINA). The relationship between the abundance and carrying capacity was strongest in parr, followed by fry, and was less in the post-smolt stage. A significant survival probability of the post-smolt stage provided an enormous abundance of the eggs and fry in the next year, and then a big abundance of parr. There

was a small effect of the density-independent factors on the abundance of the parr. The simulations showed that the high carrying capacity of fry provided a high abundance of parr, leading to a high mortality probability. Similarly, low post- smolt mortality led to a high probability of the adult returning to freshwater and caused a high mortality rate in the river.

Chapter 5

Discrete model of Atlantic salmon life cycle

5.1 Theoretical background

In this section, we collected the definitions and results we need to analyze our discrete model.

Definition 5.1.1. We call a matrix *non-negative matrix* (positive) if all its entries are non-negative (positive). In this case, we write $M \geq 0$ ($M > 0$) and this means that for all elements $\forall m_{ij} \in M$ we will have $m_{ij} \geq 0$ ($m_{ij} > 0$).

Definition 5.1.2. We call the matrix A of order $m \geq 2$ a *reducible* (also decomposable or non-connected) if there exists a permutation P that puts the matrix A into the form

$$PAP^{-1} = \begin{pmatrix} B & 0 \\ C & D \end{pmatrix}$$

where B , C , and D are square matrices. Otherwise, we say that the matrix A is *irreducible* (connected).

Definition 5.1.3. An eigenvalue λ of a square matrix A is a solution of the equation $A\vec{v} = \lambda\vec{v}$ where \vec{v} is called the right-eigenvector corresponding to the

eigenvalue λ . Similarly, the left-eigenvector associated with λ is defined as the solution of the equation $\vec{w}A = \lambda\vec{w}$.

Definition 5.1.4. The dominant eigenvalue λ_{max} of a matrix A is the eigenvalue that satisfies $|\lambda_{max}| > |\lambda_i|$ for all i .

Remark 5.1.1. The long-term dynamics of matrix models depend primarily on left eigenvectors. In particular, “the dominant left eigenvector (when it exists) has a biological interpretation as the ‘reproductive value’ of different stages, a concept due to R.A. Fisher” [13, p. 85].

Both left and right eigenvectors are used to define the eigenvalue sensitivity, that is, they determine how each matrix element influences the dominant eigenvalue. Let \vec{v} and \vec{w} be the right and left eigenvectors corresponding to the dominant eigenvalue λ_{max} of the primitive matrix A . Then, the eigenvalue sensitivity for the entries of the matrix A is calculated as follows:

$$\frac{\partial\lambda_{max}}{\partial a_{i,j}} = \frac{w_i \cdot v_j}{\vec{w} \cdot \vec{v}} \quad (5.1)$$

where w_i is the i -th component of the left eigenvector \vec{w} , v_j is the j -th component of the right eigenvector \vec{v} , and $\vec{w} \cdot \vec{v}$ is the dot product of the two eigenvectors \vec{v} and \vec{w} . The sensitivity analysis helps to determine which matrix elements have the most influence on the dominant eigenvalue λ_{max} .

However, in our model we measure fecundity and survival probability on different scales; the number of eggs may be considerably large, while the other parameters are less than 1. As a result, sensitivity values for survival probabilities are higher than the sensitivity for fecundity. This information may not be sufficient and we need to use a better tool, known as *proportional sensitivity* or *elasticity*, defined by the equation

$$e_{ij} = \frac{a_{ij}}{\lambda_{max}} \frac{w_i \cdot v_j}{\vec{w} \cdot \vec{v}}. \quad (5.2)$$

Remark 5.1.2. The value of (e_{ij}) does not specify which matrix elements or how they should be modified, but “it does identify potential targets of opportunity.

So in many applications of matrix population models, the main goal of building the model is to compute the elasticities” [13, p. 91]. Furthermore, one should remember that elasticity analysis is valid only for small changes in matrix entries, and the effect of large changes should be computed directly by modifying the matrix entries and computing the corresponding value of the dominant eigenvalue, as we do later in this thesis.

The next result summarizes a number of important properties and can be found in [18, Theorem 2].

Theorem 5.1.5. (Perron-Frobenius theorem) *Let A be a square non-negative irreducible matrix of order $n \geq 2$. Then the following hold:*

- (i) *A has a positive dominant eigenvalue λ_{max} and an associated right-eigenvector \vec{v} such that $A\vec{v} = \lambda_{max}\vec{v}$, [16, p. 53].*
- (ii) *The eigenvector x associated with the dominant eigenvalue has positive coordinates, $\vec{v} > \vec{0}$ [16, p. 53].*
- (iii) *By increasing the value of any element in the matrix A the value of the dominant eigenvalue will λ_{max} increase [15, p. 350].*

The next result is important for deciding whether a given matrix is irreducible [18, Theorem 5]. Any of the conditions listed can be used to verify that our matrix A is irreducible.

Theorem 5.1.6. (Irreducibility test) *Let $A \geq [0]$ be a square non-negative matrix of order $n \geq 2$ and let λ_{max} be its dominant eigenvalue. Then the following statements are equivalent.*

- (i) *A is irreducible.*
- (ii) *$(I + A)^{n-1} > [0]$.*
- (iii) *$(I + A + A^2 + \dots + A^{n-1}) > [0]$.*
- (iv) *$A + A^2 + \dots + A^n > [0]$.*
- (v) *A has exactly one, up to scalar multiplication, positive eigenvector and this eigenvector is associated with the dominant eigenvalue λ_{max} .*

The following irreducibility criterion can be also useful [18, Theorem 9].

Theorem 5.1.7. *Let $A \geq [0]$ be a square non-negative matrix of order $n \geq 2$. A necessary and sufficient condition for A to be irreducible is that its dominant eigenvalue λ_{max} is simple and that both A and A^T possess positive eigenvectors corresponding to λ_{max} .*

The irreducibility of the matrix is important for using Perron-Frobenius Theorem but it can be replaced with another useful property.

Definition 5.1.8. A non-negative square matrix $A = (a_{i,j})$ is said to be a power positive (primitive) matrix if there exists an integer k such that for all i, j , the (i, j) entry of A^k is positive, i.e., $A^k > 0$.

It turns out that one can avoid the verification of the irreducibility of the matrix checking that the matrix A is primitive. To this end, several tests can be used [18, Theorems 14 and 15].

Theorem 5.1.9. *An irreducible square matrix $A \geq [0]$ is primitive if and only if A^m is positive for some integer m .*

Theorem 5.1.10. *Let the matrix $A \geq [0]$ be irreducible of order n . Then the following statements are equivalent.*

- (i) A is primitive.
- (ii) $A^m > [0]$ for some positive integer m .
- (iii) $A^m > [0]$ for all $m \geq n^2 - 2n + 2$.
- (iv) $A^{n^2-2n+2} > [0]$.

We conclude by suggesting another convenient irreducibility criterion [18, Theorem 16].

Theorem 5.1.11. *A non-negative square matrix A of order m is irreducible if and only if $I + A$ is primitive.*

Finally, we note that if A is primitive, there exist no other eigenvalues of A with an absolute value equal to the unique positive eigenvalue λ_{max} , the dominant eigenvalue.

5.2 Theoretic foundations of the model

In what follows, we are concerned with a discrete model of the form (3.10) which we write again for the reader's convenience

$$N(t + 1) = AN(t). \quad (5.3)$$

The dynamics of the system describing a life cycle of Atlantic salmon is governed by an $m \times m$ matrix A , called the *projection matrix*. It consists of non-negative entries in the first row associated with the fertility of different cohorts, entries under the main diagonal associated with the survival probabilities for individuals at stage i to move to the next stage $i + 1$, and the rest of the entries are zeros. The only element affecting the transition to the next stage is the current population situation. The projection matrix includes all relevant dynamical information. It offers an overview of how population composition changes from one moment to the next due to survival, growth, development, and reproduction. A straightforward way to determine whether a population will grow or be extinct over time through the matrix model is to know the behavior of the powers of the projection matrix A^t , which can be explored with the help of the eigenvalues and eigenvectors of the matrix A .

We say that the population reached a *stable age distribution* at time t_0 , if there exists a constant $\lambda > 0$ such that the equation

$$N(t + 1) = \lambda N(t) \quad (5.4)$$

is satisfied for all $t > t_0$. Such λ is called the population growth rate. It follows from equation (5.3) that the stable age distribution is achieved if and only if

$$AN(t) = \lambda N(t). \quad (5.5)$$

Therefore, we are interested in finding positive eigenvalues of the matrix A . Theorem 5.1.5 assures that a positive eigenvalue exists and Theorem 5.1.6

guarantees that it is unique. The eigenvalues can be found by solving the characteristic equation for the matrix A :

$$P_{ch}(\lambda) = \lambda^m - f_1\lambda^{m-1} - \sum_{k=2}^m p_1 p_2 \dots p_{k-1} f_k \lambda^{m-k} = 0. \quad (5.6)$$

The population long-term fate is determined by the dominant eigenvalue and associated right eigenvector. If we have m eigenvalues and the corresponding linearly independent eigenvectors are \vec{v}_m , given the initial vector $N(0)$, we can find from (5.3) constants c_i such that the following expansion for $N(0)$ holds:

$$N(0) = c_1 \vec{v}_1 + c_2 \vec{v}_2 + \dots + c_m \vec{v}_m = \sum_i^m c_i \vec{v}_i. \quad (5.7)$$

Then

$$\begin{aligned} N(1) &= A(c_1 \vec{v}_1 + c_2 \vec{v}_2 + \dots + c_m \vec{v}_m) \\ &= A c_1 \vec{v}_1 + A c_2 \vec{v}_2 + \dots + A c_m \vec{v}_m \\ &= c_1 \lambda_1 \vec{v}_1 + c_2 \lambda_2 \vec{v}_2 + \dots + c_m \lambda_m \vec{v}_m. \end{aligned} \quad (5.8)$$

Similarly, for $N(2)$ we have

$$N(2) = c_1 \lambda_1^2 \vec{v}_1 + c_2 \lambda_2^2 \vec{v}_2 + \dots + c_m \lambda_m^2 \vec{v}_m \quad (5.9)$$

and

$$N(t) = \sum_i^m c_i \lambda_i^t \vec{v}_i. \quad (5.10)$$

It follows from equation (5.10) that the dominant eigenvalue is the maximal one, and it has the biggest influence on the fate of the population,

$$N(t) \sim c_1 \lambda_{max}^t \vec{v}_1 \quad (5.11)$$

where λ_{max} is the dominant eigenvalue. We say that we have reached a stable stage distribution if, in the long term, the population grows exponentially at the rate of the dominant eigenvalue, and the population vector becomes

proportional to the eigenvector \vec{v}_1 and relative population numbers at each stage become constant.

The following result is taken from the paper by Anderson [4, Theorem 1].

Theorem 5.2.1. *The growth rate λ in equation (5.4) is between $R_0^{1/(k-m+l)}$ and $R_0^{1/k}$.*

We summarize the most important information regarding the analysis of discrete models in Table 5.1.

Model	$N(t + 1) = AN(t), N(0) = N_0$
Solutions	$N(t) = A^t N_0$
Eigenmode expansion	$N(t) = \sum c_i \lambda_i \vec{v}_i$
Long-term exponential growth	$\sum N_i(t) \approx c \lambda^t$ as $t \rightarrow \infty$
Stable stage distribution	$N(t) \approx c \lambda^t \vec{v}$
Eigenvalue sensitivity	$\frac{\partial \lambda_{max}}{\partial a_{i,j}} = \frac{w_i \cdot v_j}{\vec{w} \cdot \vec{v}}$
Elasticity	$e_{ij} = \frac{a_{ij}}{\lambda_{max}} \frac{w_i \cdot v_j}{\vec{w} \cdot \vec{v}}$

Table 5.1: Basic properties of models with a primitive projection matrix

5.3 Where do our data come from?

Due to the lack of the data from the oceanic stage, we concentrate our attention to the river stages. The main source of data we used is the paper “*Inter-stage survival of wild juvenile Atlantic salmon*” [12], especially Table 6 which contains the estimates for survival probabilities for each of the stages in the river. In order to build our model, we have combined information from several sources; most of them are taken from the paper [12] and tables therein providing estimated survival probability for each stage across different years. We took the

average values of all parameters to construct our model despite the fact that this may not be realistic since the parameters are changing significantly from year to year, this is the parameter error. A good news is that we have tested the model for persistence using minimal possible values of all parameters. As we will see later, salmon exhibits very high flexibility that allows it to survive even if it faces disastrous situations at some stages. For easy reference, we have included the Tables 3, 5, and 6 in the appendix. We also used some important parameters from IBSEM model like the percentage of the surviving of the adults after spawning. The next table [12, Table 6] illustrates the probability for individuals at each stage to survive to the next stage, the average values are used as reference values in our model.

Cohort	Egg to 0+	0+ to 1+	1+ to 2+	1+ to S2	2+ to S3, S4
1986					
1987					18,3
1988			47,7	4	22,4
1989		74,7	25,9	0,3	7,6
1990	61	23,5	28,7	0,5	9,3
1991	24,9	32,4	42,9	1,2	12,4
1992	17,7	35,4	30,3	0,2	7,5
1993	53,9	19,8	25,5	0,3	
1994	17,3	14			
1995	9,2				
Average	30,7	33,3	33,5	1,1	12,9
n	6	6	6	6	6
Standard deviation	21,451216	21,772	9,4344	1,474337	6,162278

Table 5.2: Survival probability at different stages

Constructing the model for Atlantic salmon life cycle, we must find a balance between model errors and parameter errors. In general, the model error shows that the model's assumptions are inaccurate, that the model ignores some critical facts, or is too simplified. Parameter errors arise when parameters are approximated from limited data set. The model error can be reduced by making a model more complicated, but in this case parameter error usually increases since we have to estimate more parameters from the same data set. In our case, we do not have a complete large set of all relevant biological parameters and we also have to assume that the values of parameters in the

saltwater (not available to us) and in freshwater (available to us) are the same. We also assume that all adults are combined in one cohort only and that they have the same fecundity which does not fully correspond to the reality.

5.4 Discrete model for Atlantic salmon life cycle

We begin with a Figure 5.1 showing the life cycle of salmon.

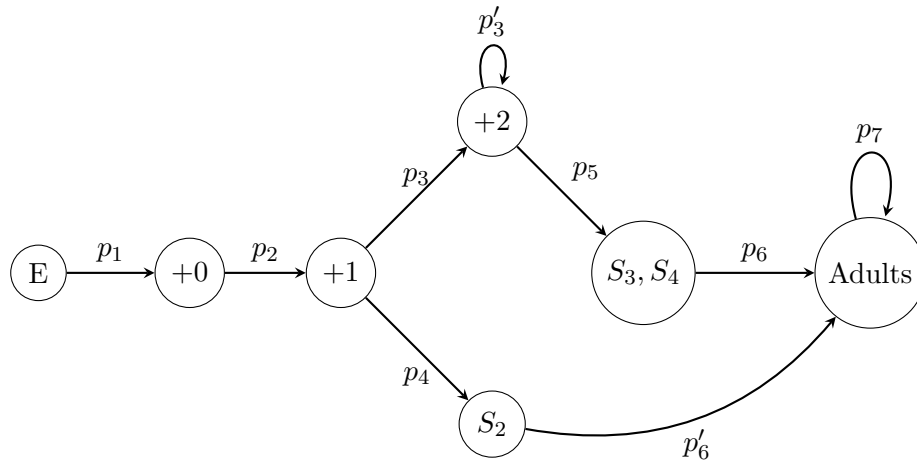


Figure 5.1: The transition between age stages

The arrows between stages represent the transition between stages, i.e., the probability that an individual from the stage i will survive to the stage $i + 1$ in the period from the time t to time $t + 1$, while the loop arrows represent the probability that the individual will survive and remain at the same stage in the same period.

Remark 5.4.1. This model is not the Leslie model because we have stages instead of the age, and the survival probability is not the same for individuals of the same age which are at different stages.

We have the following variables and parameters in our model: $N_1(t)$ the number of eggs at time t ; $N_2(t)$ the number of parr (0+) at time t ; $N_3(t)$ the number of parr (1+) at time t ; $N_4(t)$ the number of parr (2+) at time t ; $N_5(t)$ the number of smolt (S_2) at time t ; $N_6(t)$ the number of smolt (S_3, S_4) at time t ;

$N_7(t)$ the number of adults at time t ; $N_1(t + 1)$ the number of eggs at time $t + 1$; f_1 the fertility of eggs; f_2 the fertility of parr (0+); f_3 the fertility of parr (1+); f_4 the fertility of parr (2+); f_5 the fertility of smolt (S_2); f_6 the fertility of smolt (S_3, S_4); f_7 the fertility of adults; p_1 the survival rate of eggs that grow to parr (0+); p_2 the survival rate of parr (0+) to parr (1+); p_3 the survival rate of parr (1+) to parr (2+); p'_3 the proportion of the parr (2+) which stay at the same stage; p_5 the survival rate of parr (2+) to smolt (S_3, S_4); p_6 the survival rate of smolt (S_3, S_4) to adult; p'_6 the rate of transition from smolt (S_2) to adult; p_7 the probability for adults to survive after spawning.

With this notation our system can be written as

$$\begin{aligned}
N_1(t + 1) &= f_1 \cdot N_1(t) + f_2 \cdot N_2(t) + f_3 \cdot N_3(t) + f_4 \cdot N_4(t) \\
&\quad + f_5 \cdot N_5(t) + f_6 \cdot N_6(t) + f_7 \cdot N_7(t), \\
N_2(t + 1) &= p_1 \cdot N_1(t), \\
N_3(t + 1) &= p_2 \cdot N_2(t), \\
N_4(t + 1) &= p_3 \cdot N_3(t) + p'_3 \cdot N_4(t), \\
N_5(t + 1) &= p_4 \cdot N_3(t), \\
N_6(t + 1) &= p_5 \cdot N_4(t), \\
N_7(t + 1) &= p_6 \cdot N_5(t) + p'_6 \cdot N_6(t) + p_7 \cdot N_7(t).
\end{aligned}$$

We note that the data were approximated in the IBSEM model suggested by Castellani et al. [9] where the smolting probabilities of individuals longer than the 90 mm threshold are calculated using a logistic function of size (Fig A in S2 File in [9]). The function was parameterized in order to fit the size distribution of pre-smolts found in the river Os by Rådgivende Biologer AS [24] in October 2010. The parameterization gives a 50% smolting probability for parr of 103 mm length.

We also use the data from the paper [12, Tables 5 and 6, p. 12] to calculate survival rates, fecundity rates and the number of salmon at different age stages.

The survival probability of the eggs is 30.7%, so $p_1 = 0.307$.

The survival probability of the parr (0+) to parr (1+) is 33.3%, so $p_2 = 0.333$.
The survival probability of the parr (1+) to parr (2+) is 33.5%, so $p_3 = 0.335$.
The survival probability of the parr (1+) to smolt (S_2) is 1.1%, so $p_4 = 0.011$.
The survival probability of the parr (2+) to smolt (S_3, S_4) is 12.9%, so $p_5 = 0.129$.

The survival probability of the smolt: We assume that the mortality rate of smolt is 90% [3, p.4] then $p_6 = 0.1$.

The proportion of the transition from smolt (S_2) to adult $p'_6 = 0.1$ based on the the survival of smolt in the sea, which is about 10%

According to Fleming [14, p. 26], females lose 50% and males more than 90% of their energy due to reproduction. This is why the proportion of females is much greater than males in the fish, which repeat the spawning. The adult proportion that survives after spawning varies between 10% and 40% in some rivers. Then we will take $p_7 = 20\% = 0.20$ as the survival probability of adults after spawning in one of our experiments, but we will use the survival probability $p_7 = 0.05$ as in the IBSEM model, which assume that 95% of adults die after spawning.

$f_1 = 0$ since eggs do not reproduce.

$f_2 = 0$ we assume that the small parr (0+) do not reproduce.

$f_5 = 0$ and $f_6 = 0$ the smolt do not reproduce since they travel to the ocean.

Based on the Table 5 and 6 from [12] we calculated the number of eggs laid by each female as follows. The average proportion of females among the adult spawners was 14,5% for grils (the fish spend one year at sea) and 78.5% for MSW (multi sea winter, that is, the fish that spend more than one year in the ocean). In the year 1990, there were 83 grils and 28 MSW, but because that some fish escapes the trapping fence, so we did apply a correction for 1.1 of the number of the adults, and this number is the average correction of all other years. So we get, by the correction of the numbers of the adults: $83 \times 1.1 = 91.3$ grils and $28 \times 1.1 = 30.8$ MSW. By taking the percentage of females from the total number of adults we will have $91.3 \times 0.145 = 13.23$

the number of females in grils, and similarly, $30.8 \times 0.785 = 24.178$ females in MSW. Then the total number of females is $13.23 + 24.178 = 37.5$. From table [A.1](#), the total number of eggs in the year 1990 was 269,256. Then

$$f_7 = \text{The number of eggs laid by each female}$$

$$= \frac{\text{Total number of eggs}}{\text{The number of females}} = \frac{269256}{37.5} = 7180.16.$$

Table [5.3](#) collects all parameters in our model which are used as reference values in all numerical experiments.

f_7	p_1	p_2	p_3	p'_3	p_4	p_5	p_6	p'_6	p_7
7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.05

Table 5.3: Parameters in our model.

Using parameters listed in Table [5.3](#), we can write the system of discrete equations governing our model as

$$\begin{pmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \\ N_5 \\ N_6 \\ N_7 \end{pmatrix} (t+1) = \begin{pmatrix} f_1 & f_2 & f_3 & f_4 & f_5 & f_6 & f_7 \\ p_1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & p_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & p_3 & p'_3 & 0 & 0 & 0 \\ 0 & 0 & p_4 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & p_5 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & p_6 & p_6 & p_7 \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \\ N_5 \\ N_6 \\ N_7 \end{pmatrix} (t)$$

$$= \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 7180.16 \\ 0.307 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.333 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.335 & 0.05 & 0 & 0 & 0 \\ 0 & 0 & 0.011 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.129 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.1 & 0.1 & 0.05 \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \\ N_5 \\ N_6 \\ N_7 \end{pmatrix} (t).$$

Our population projection matrix in the general case is given by

$$A_{gen} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & a \\ b & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & c & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & d & e & 0 & 0 & 0 \\ 0 & 0 & f & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & g & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & h & i & j \end{pmatrix}.$$

The characteristic polynomial is given by:

$$P_{gen}(\lambda) = \lambda^7 + (-e - j) \lambda^6 + e j \lambda^5 - a b c f h \lambda^2 + (a b c e f h - a b c d g i) \lambda. \quad (5.12)$$

Computing the powers of A_{gen} , we establish the following result.

Theorem 5.4.1. *The matrix A_{gen} is primitive provided all its entries are non-negative.*

Proof. A straightforward computation gives

$$E = A_{gen}^7 = \begin{pmatrix} E_{1,1} & E_{1,2} & E_{1,3} & E_{1,4} & E_{1,5} & E_{1,6} & E_{1,7} \\ E_{2,1} & E_{2,2} & E_{2,3} & E_{2,4} & E_{2,5} & E_{2,6} & E_{2,7} \\ E_{3,1} & E_{3,2} & E_{3,3} & E_{3,4} & E_{3,5} & E_{3,6} & E_{3,7} \\ E_{4,1} & E_{4,2} & E_{4,3} & E_{4,4} & E_{4,5} & E_{4,6} & E_{4,7} \\ E_{5,1} & E_{5,2} & E_{5,3} & E_{5,4} & E_{5,5} & E_{5,6} & E_{5,7} \\ E_{6,1} & E_{6,2} & E_{6,3} & E_{6,4} & E_{6,5} & E_{6,6} & E_{6,7} \\ E_{7,1} & E_{7,2} & E_{7,3} & E_{7,4} & E_{7,5} & E_{7,6} & E_{7,7} \end{pmatrix}$$

where all entries except for $E_{5,1}$ are positive: $E_{1,1} = a b c f h j^2 + a b c d g i j + a b c d e g i$; $E_{1,2} = a j^2 (c d g i + c f h j) + a c d e^2 g i + a c d e g i j$; $E_{1,3} = a j^2 (f h j^2 + d g i j + d e g i) + a d e^3 g i + a d e^2 g i j$; $E_{1,4} = a j^2 (g i e^2 + g i e j + g i j^2) + a e^4 g i + a e^3 g i j$; $E_{1,5} = b c f a^2 h^2 + a h j^5$; $E_{1,6} =$

$bcfhia^2 + ia j^5$; $E_{1,7} = 2bcfha^2 j + bcdgia^2 + a j^6$; $E_{2,1} = ab^2cdgi + ab^2cfhj$; $E_{2,2} = abj(cdgi + cfhj) + abcdegi$; $E_{2,3} = abj(fhj^2 + dgi j + degi) + abde^2gi$; $E_{2,4} = abj(gie^2 + gie j + gij^2) + abe^3gi$; $E_{2,5} = abhj^4$; $E_{2,6} = abij^4$; $E_{2,7} = cfha^2b^2 + abj^5$; $E_{3,1} = ab^2c^2fh$; $E_{3,2} = abc(cdgi + cfhj)$; $E_{3,3} = abc(fhj^2 + dgi j + degi)$; $E_{3,4} = abc(gie^2 + gie j + gij^2)$; $E_{3,5} = abchj^3$; $E_{3,6} = abci j^3$; $E_{3,7} = abcj^4$; $E_{4,1} = bcde^4$; $E_{4,2} = abdfhc^2 + dce^5$; $E_{4,3} = de^6 + abcd f h e + bcd(adgi + afhj)$; $E_{4,4} = e^7 + bcd(aegi + agij) + abcdegi$; $E_{4,5} = abcdhe^2 + abcdhej + abcdhj^2$; $E_{4,6} = abcdie^2 + abcdiej + abcdij^2$; $E_{4,7} = abcde^3 + abcde^2j + abcdej^2 + abcdj^3$; $E_{5,1} = \mathbf{0}$; $E_{5,2} = abc^2f^2h$; $E_{5,3} = bcf(adgi + afhj)$; $E_{5,4} = bcf(aegi + agij)$; $E_{5,5} = abcfhj^2$; $E_{5,6} = abcfij^2$; $E_{5,7} = abcfj^3$; $E_{6,1} = bcde^3g$; $E_{6,2} = cde^4g$; $E_{6,3} = dge^5 + abcd f gh$; $E_{6,4} = e^6g + abcdig^2$; $E_{6,5} = abcdegh + abcdghj$; $E_{6,6} = abcdegi + abcdgij$; $E_{6,7} = abcdge^2 + abcdgej + abcdgj^2$; $E_{7,1} = bcde(egi + gij) + bcfhj^3 + bcdgij^2$; $E_{7,2} = j^3(cdgi + cfhj) + cde^2(egi + gij) + cdegij^2$; $E_{7,3} = j^3(fhj^2 + dgi j + degi) + de^3(egi + gij) + abc f^2 h^2 + de^2gij^2$; $E_{7,4} = j^3(gie^2 + gie j + gij^2) + e^4(egi + gij) + e^3gij^2 + abcfghi$; $E_{7,5} = hj^6 + abch(dgi + fhj) + abcfh^2j$; $E_{7,6} = ij^6 + abci(dgi + fhj) + abcfhij$; $E_{7,7} = j^7 + abcd(egi + gij) + abcj(dgi + fhj) + 2abcfhj^2$.

Finally,

$$F = A_{gen}^8 = \begin{pmatrix} F_{1,1} & F_{1,2} & F_{1,3} & F_{1,4} & F_{1,5} & F_{1,6} & F_{1,7} \\ F_{2,1} & F_{2,2} & F_{2,3} & F_{2,4} & F_{2,5} & F_{2,6} & F_{2,7} \\ F_{3,1} & F_{3,2} & F_{3,3} & F_{3,4} & F_{3,5} & F_{3,6} & F_{3,7} \\ F_{4,1} & F_{4,2} & F_{4,3} & F_{4,4} & F_{4,5} & F_{4,6} & F_{4,7} \\ F_{5,1} & F_{5,2} & F_{5,3} & F_{5,4} & F_{5,5} & F_{5,6} & F_{5,7} \\ F_{6,1} & F_{6,2} & F_{6,3} & F_{6,4} & F_{6,5} & F_{6,6} & F_{6,7} \\ F_{7,1} & F_{7,2} & F_{7,3} & F_{7,4} & F_{7,5} & F_{7,6} & F_{7,7} \end{pmatrix}$$

where all entries are positive: $F_{1,1} = bcde(aegi + agij) + abc f h j^3 + abcdgij^2$; $F_{1,2} = aj^3(cdgi + cfhj) + cde^2(aegi + agij) + acdegij^2$; $F_{1,3} = aj^3(fhj^2 + dgij + degi) + de^3(aegi + agij) + a^2bcf^2h^2 + ade^2gij^2$; $F_{1,4} = e^4(aegi + agij) + aj^3(gie^2 + gie j + gij^2) + ae^3gij^2 + a^2bcfghi$; $F_{1,5} = ahj^6 + abch(adgi + afhj) + a^2bcfh^2j$; $F_{1,6} = aij^6 + abci(adgi + afhj) + a^2bcfhij$; $F_{1,7} = aj^7 + abcd(aegi + agij) + abcj(adgi + afhj) + 2a^2bcfhj^2$; $F_{2,1} = acf h b^2 j^2 + acd gib^2 j + acdegib^2$; $F_{2,2} = abj^2(cdgi + cfhj) + abcde^2gi + abcdegij$; $F_{2,3} = abj^2(fhj^2 + dgij + degi) + abde^3gi + abde^2gij$; $F_{2,4} = abj^2(gie^2 + gie j + gij^2) + abe^4gi + abe^3gij$; $F_{2,5} = cfa^2b^2h^2 + abhj^5$; $F_{2,6} = cfhia^2b^2 + iabj^5$; $F_{2,7} = 2cfha^2b^2j + cdgia^2b^2 + abj^6$; $F_{3,1} = ab^2c^2dgi + ab^2c^2fhj$; $F_{3,2} = abcj(cdgi + cfhj) + abc^2degi$; $F_{3,3} = abcj(fhj^2 + dgij + degi) + abcde^2gi$; $F_{3,4} = abcj(gie^2 + gie j + gij^2) + abce^3gi$; $F_{3,5} = abchj^4$; $F_{3,6} = abcij^4$; $F_{3,7} = fha^2b^2c^2 + abcj^5$; $F_{4,1} = adf h b^2 c^2 + dbce^5$; $F_{4,2} = cde^6 + abcd(cdgi + cfhj) + abc^2defh$; $F_{4,3} = de^7 + abcd(fhj^2 + dgij + degi) + bcde(adgi + afhj) + abcde^2fh$; $F_{4,4} = e^8 + abcd(gie^2 + gie j + gij^2) + bcde(aegi + agij) + abcde^2gi$; $F_{4,5} = abcdhe^3 + abcdhe^2j + abcdhej^2 + abcdhj^3$; $F_{4,6} = abcdie^3 + abcdie^2j + abcdiej^2 + abcdij^3$; $F_{4,7} = abcde^4 + abcde^3j + abcde^2j^2 + abcdej^3 + abcdj^4$; $F_{5,1} = ab^2c^2f^2h$; $F_{5,2} = abcf(cdgi + cfhj)$; $F_{5,3} = abcf(fhj^2 + dgij + degi)$; $F_{5,4} = abcf(gie^2 + gie j + gij^2)$; $F_{5,5} = abc f h j^3$; $F_{5,6} = abc f i j^3$; $F_{5,7} = abc f j^4$; $F_{6,1} = bcde^4g$; $F_{6,2} = abdfghc^2 + dgce^5$; $F_{6,3} = dge^6 + abcd f g h e + bcdg(adgi + afhj)$; $F_{6,4} = e^7g + bcdg(aegi + agij) + abcdeg^2i$; $F_{6,5} = abcdghe^2 + abcdghej + abcdghj^2$; $F_{6,6} = abcdgie^2 + abcdgiej + abcdgij^2$; $F_{6,7} = abcdge^3 + abcdge^2j + abcdgej^2 + abcdgj^3$; $F_{7,1} = bcde(gie^2 + gie j + gij^2) + bc f h j^4 + bcdgij^3$; $F_{7,2} = j^4(cdgi + cfhj) + cde^2(gie^2 + gie j + gij^2) + abc^2f^2h^2 + cdegij^3$; $F_{7,3} = j^4(fhj^2 + dgij + degi) + de^3(gie^2 + gie j + gij^2) + de^2gij^3 + bcfh(adgi + afhj) + abfh(cdgi + cfhj)$;

$F_{7,4} = e^4 (gie^2 + giej + gij^2) + j^4 (gie^2 + giej + gij^2) + e^3 gij^3 + bcfh (aegi + agij) + abgi (cdgi + cfhj);$ $F_{7,5} = hj^7 + abch (fhj^2 + dgij + degi) + abhj (cdgi + cfhj) + abc fh^2 j^2;$
 $F_{7,6} = ij^7 + abci (fhj^2 + dgij + degi) + abij (cdgi + cfhj) + abc fhij^2;$
 $F_{7,7} = j^8 + abj^2 (cdgi + cfhj) + abcd (gie^2 + giej + gij^2) + abcj (fhj^2 + dgij + degi) + 2abc fhj^3.$ Thus, all entries in A_{gen}^8 are positive and thus A_{gen} is a primitive matrix irrelevant of the choice of its non-zero entries. \square

5.5 Properties of the population projection matrix

Recall that the population projection matrix A in the model is given by

$$A = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 7180.16 \\ 0.307 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.333 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.335 & 0.5 & 0 & 0 & 0 \\ 0 & 0 & 0.011 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.129 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.1 & 0.1 & 0.05 \end{pmatrix}.$$

The characteristic equation for the matrix A is as follows:

$$\lambda^7 - 0.55 \lambda^6 + 0.025 \lambda^5 - 0.80742044 \lambda^2 - 2.7683511 \lambda = 0. \quad (5.13)$$

The spectral radius is equal to 1.3607 and the eigenvalues are

$$\begin{aligned} \lambda_1 &= 1.36069, & \lambda_2 &= 0.66383 + 1.0741i, \\ \lambda_3 &= 0.66383 - 1.0741i, & \lambda_4 &= -0.55072 + 0.96303i, \\ \lambda_5 &= -0.55072 - 0.96303i, & \lambda_6 &= -1.03691, \\ \lambda_7 &= -3.3552 \cdot 10^{-16}. \end{aligned}$$

The right-eigenvectors \vec{v}_i corresponding to eigenvalues λ_i are given by

$$\vec{v}_1 = \begin{pmatrix} 0.97385 \\ 0.21972 \\ 0.05377 \\ 0.02093 \\ 0.00043 \\ 0.00198 \\ 0.00018 \end{pmatrix}, \quad \vec{v}_2 = \begin{pmatrix} 0.96963 \\ 0.12395 - 0.20054i \\ -0.027804 - 0.055613i \\ -0.018244 + 0.0058894i \\ -0.00053948 - 4.8672 \cdot 10^{-5}i \\ -0.00046813 + 0.0019019i \\ 8.9647 \cdot 10^{-5} + 0.00014505i \end{pmatrix},$$

$$\vec{v}_3 = \begin{pmatrix} 0.96963 \\ 0.12395 + 0.20054i \\ -0.027804 + 0.055613i \\ -0.018244 - 0.0058894i \\ -0.00053948 + 4.8672e - 05i \\ -0.00046813 - 0.0019019i \\ 8.9647 \cdot 10^{-5} - 0.00014505i \end{pmatrix},$$

$$\vec{v}_4 = \begin{pmatrix} 0.96053 \\ -0.13195 - 0.23074i \\ -0.040463 + 0.068766i \\ 0.017932 - 0.0054892i \\ 0.00079107 + 9.8017 \cdot 10^{-6}i \\ -0.0015892 - 0.0014932i \\ -7.3674 \cdot 10^{-5} + 0.00012883i \end{pmatrix}, \quad \vec{v}_5 = \begin{pmatrix} 0.96053 \\ -0.13195 + 0.23074i \\ -0.040463 - 0.068766i \\ 0.017932 + 0.0054892i \\ 0.00079107 - 9.8017 \cdot 10^{-6}i \\ -0.0015892 + 0.0014932i \\ -7.3674 \cdot 10^{-5} - 0.00012883i \end{pmatrix},$$

$$\vec{v}_6 = \begin{pmatrix} -0.95471 \\ 0.28266 \\ -0.090775 \\ 0.019786 \\ 0.00096298 \\ -0.0024616 \\ 0.00013788 \end{pmatrix}, \quad \vec{v}_7 = \begin{pmatrix} 9.0883 \cdot 10^{-14} \\ 2.3667 \cdot 10^{-14} \\ -2.0827 \cdot 10^{-14} \\ 6.5085 \cdot 10^{-15} \\ 0.70711 \\ -0.70711 \\ -4.4376 \cdot 10^{-17} \end{pmatrix}.$$

The left-eigenvectors \vec{w}_i are

$$\vec{w}_1 = \begin{pmatrix} 0.00018156 \\ 0.00080470 \\ 0.00328810 \\ 0.01095534 \\ 0.07309381 \\ 0.07309381 \\ 0.99457683 \end{pmatrix}, \quad \vec{w}_2 = \begin{pmatrix} 8.4956 \cdot 10^{-5} + 0.00014865i \\ -0.00033637 + 0.00061866i \\ -0.002666 + 0.00014835i \\ -0.0071172 - 0.0060553i \\ 0.041378 - 0.066948i \\ 0.041378 - 0.066948i \\ 0.99374 \end{pmatrix},$$

$$\vec{w}_3 = \begin{pmatrix} 8.4956 \cdot 10^{-5} - 0.00014865i \\ -0.00033637 - 0.00061866i \\ -0.002666 - 0.00014835i \\ -0.0071172 + 0.0060553i \\ 0.041378 + 0.066948i \\ 0.041378 + 0.066948i \\ 0.99374 \end{pmatrix}, \quad \vec{w}_4 = \begin{pmatrix} -8.2991 \cdot 10^{-5} + 0.00013305i \\ -0.00026848 - 0.000499i \\ 0.0018871 + 4.8812 \cdot 10^{-5}i \\ -0.0017851 + 0.0078934i \\ -0.044387 - 0.077619i \\ -0.044387 - 0.077619i \\ 0.99194 \end{pmatrix},$$

$$\vec{w}_5 = \begin{pmatrix} -8.2991 \cdot 10^{-5} - 0.00013305i \\ -0.00026848 + 0.000499i \\ 0.0018871 - 4.8812 \cdot 10^{-5}i \\ -0.0017851 - 0.0078934i \\ -0.044387 + 0.077619i \\ -0.044387 + 0.077619i \\ 0.99194 \end{pmatrix}, \quad \vec{w}_6 = \begin{pmatrix} 0.00014999 \\ -0.00050659 \\ 0.00157745 \\ -0.00802014 \\ 0.09555236 \\ 0.09555236 \\ -0.99079382 \end{pmatrix},$$

$$\vec{w}_7 = \begin{pmatrix} 1.4684 \cdot 10^{-19} \\ -1.0069 \cdot 10^{-18} \\ -4.699 \cdot 10^{-18} \\ -0.032556 \\ 0.99147 \\ 0.12619 \\ 2.0407 \cdot 10^{-15} \end{pmatrix}.$$

To check that the matrix A is primitive, we apply Theorem 5.4.1 which assures this. In fact, the direct computation yields

$$A^7 = \begin{pmatrix} 1.74665 & 2.86758 & 4.30911 & 6.43202 & 579.72810 & 579.72810 & 23355.12807 \\ 0.98622 & 1.74665 & 2.64369 & 3.94890 & 0.00138 & 0.00138 & 1779.76526 \\ 0.08254 & 1.06974 & 1.74665 & 2.62760 & 0.00918 & 0.00918 & 0.00459 \\ 0.00214 & 0.09356 & 1.21664 & 3.33848 & 6.82362 & 6.82362 & 34.14884 \\ \mathbf{0} & 0.00296 & 0.03534 & 0.05729 & 0.00202 & 0.00202 & 0.00101 \\ 0.00055 & 0.00090 & 0.03624 & 0.41121 & 1.74463 & 1.74463 & 8.80247 \\ 0.00012 & 0.00020 & 0.00119 & 0.01086 & 0.32528 & 0.32528 & 1.90929 \end{pmatrix},$$

and finally,

$$A^8 = \begin{pmatrix} 0.88035 & 1.43494 & 8.53174 & 78.00093 & 2335.51281 & 2335.51281 & 13708.71965 \\ 0.53622 & 0.88035 & 1.32290 & 1.97463 & 177.97653 & 177.97653 & 7170.02432 \\ 0.32841 & 0.58164 & 0.88035 & 1.31499 & 0.00046 & 0.00046 & 592.66183 \\ 0.02872 & 0.40514 & 1.19345 & 2.54949 & 3.41488 & 3.41488 & 17.07596 \\ 0.00091 & 0.01177 & 0.01921 & 0.02890 & 0.00010 & 0.00010 & 0.00005 \\ 0.00028 & 0.01207 & 0.15695 & 0.43066 & 0.88025 & 0.88025 & 4.40520 \\ 0.00006 & 0.00040 & 0.00722 & 0.04739 & 0.19093 & 0.19093 & 0.97581 \end{pmatrix}.$$

This confirms that the matrix A is primitive.

5.6 Numerical simulations

Sensitivity analysis

Sensitivity analysis of all elements in the reference model facilitated with the help of Matlab yields the following results:

$$\frac{\partial \lambda_{max}}{\partial a_{i,j}} = \frac{w_i \cdot v_j}{\vec{w} \cdot \vec{v}} =$$

$$= \begin{pmatrix} 0.1512 & 0.0350 & 0.0088 & 0.0036 & 0.0001 & 0.0003 & 2.790 \cdot 10^{-5} \\ 0.6526 & 0.1512 & 0.0380 & 0.0154 & 0.0003 & 0.0015 & 0.0001 \\ 2.5963 & 0.6016 & 0.1512 & 0.0614 & 0.0013 & 0.0060 & 0.0005 \\ 10.0562 & 2.3304 & 0.5858 & 0.2379 & 0.0049 & 0.0232 & 0.0019 \\ 6.4297 & 1.4900 & 0.3745 & 0.1521 & 0.0031 & 0.0148 & 0.0012 \\ 64.2965 & 14.8997 & 3.7452 & 1.5212 & 0.0311 & 0.1481 & 0.0119 \\ 851.7952 & 197.3903 & 49.6161 & 20.1522 & 0.4120 & 1.9623 & 0.1572 \end{pmatrix}.$$

Eliminating elements associated with zero entries in the matrix A , we collect sensitivity for all non-zero entries of A

$$\frac{\partial \lambda_{max}}{\partial a_{i,j}} = \frac{w_i \cdot v_j}{\vec{w} \cdot \vec{v}} =$$

$$= \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 2.7903 \cdot 10^{-5} \\ 0.6526 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.6016 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.5858 & 0.2379 & 0 & 0 & 0 \\ 0 & 0 & 0.3745 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1.5212 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.4120 & 1.9623 & 0.1572 \end{pmatrix}.$$

Thus, we have

$$\begin{aligned} \frac{\partial \lambda}{\partial a_{1,7}} &= 2.7903 \cdot 10^{-5} & \frac{\partial \lambda}{\partial a_{2,1}} &= 0.69964, \\ \frac{\partial \lambda}{\partial a_{3,2}} &= 0.64502 & \frac{\partial \lambda}{\partial a_{4,3}} &= 0.52594, \\ \frac{\partial \lambda}{\partial a_{4,4}} &= 0.20471, & \frac{\partial \lambda}{\partial a_{5,3}} &= 3.5091, \\ \frac{\partial \lambda}{\partial a_{6,4}} &= 1.3658, & \frac{\partial \lambda}{\partial a_{7,5}} &= 0.386, \\ \frac{\partial \lambda}{\partial a_{7,6}} &= 1.7619, & \frac{\partial \lambda}{\partial a_{7,7}} &= 0.16388. \end{aligned}$$

Sensitivity analysis allows us to conclude the following.

- (i) The sensitivity of the parameter $a_{1,7} = f_7$ corresponding the fecundity i.e., the number of eggs laid by each female, is very small because the number of eggs is very large, therefore the change of the number of eggs does not have a big influence on the population fate.
- (ii) The largest number in the sensitivity analysis corresponds to the parameter p_4 which is the probability of the parr +1 to survive to become smolt S_2 , which means that the number of parr in the stage +1 is influencing the size of the population.
- (iii) The sensitivity of the second parameter p_1 which is the probability of the eggs to survive to the parr 0+ was 0.69964 which is not too big, but still has significant impact on the dynamics of the population, because at this stage the mortality is high and transition to the next stage is important.

(iv) The second largest sensitivity number is for the parameter p'_6 which is the probability of the smolts S_3, S_4 to become adults, and this is important because adults are harvested and should be replenished with smolts.

To understand what parameters influence most the fate of the population, we calculate the elasticity of the elements of our matrix

$$e_{ij} = \frac{a_{ij}}{\lambda_{max}} \cdot \frac{w_i \cdot v_j}{W \cdot \bar{v}} =$$

$$= \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0.15785 \\ 0.15785 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.15785 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.12949 & 0.07522 & 0 & 0 & 0 \\ 0 & 0 & 0.02837 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.12949 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.02837 & 0.12949 & 0.00602 \end{pmatrix}.$$

Table 5.4 summarizes the outcomes of the sensitivity and elasticity analyses for each non-zero parameter in our model.

Parameter	Sensitivity	Elasticity
f_1	$2.790 \cdot 10^{-5}$	0.15785
p_1	0.6526	0.15785
p_2	0.6016	0.15785
p_3	0.5858	0.12949
p'_3	0.2379	0.07522
p_4	0.3745	0.02837
p_5	1.5212	0.12949
p_6	0.4120	0.02837
p'_6	1.9623	0.12949
p_7	0.1572	0.00602

Table 5.4: Eigenvalue sensitivity and elasticity analyses

Testing the model for persistence

The life cycle of Atlantic salmon is affected by many environmental and genetic factors, as well as by human activities. To test the persistence of

our simple model to external perturbations which may change the values of model parameters, we ran a series of numerical experiments where numerous tests were combined to determine how sensitive is the salmon population to changes of the environment. Our numerical experiments were designed to find for each parameter the minimal values that ensure that the dominant eigenvalue remains larger than unity (but very close to it) given that one or more parameters in the model are fixed (these are marked red in Table 5.6). These threshold values draw “red lines” that should not be crossed to ensure the sustainability of Atlantic salmon population.

Each row in Table 5.6 collects information about a multiple number of single numerical tests exemplified in Table 5.5. First we use Table 5.5 to explain how single numerical tests were performed. For this series of tests, we fixed for all tests the value of the parameter $p_7 = 0$. Recall that p_7 represents the survival probability of the adults after spawning, and we assume that no adult survives after spawning. Keeping all other parameters set as in the reference model and fixed, we start testing them one by one as explained below. In the first test, we explored the impact of variation of the parameter f_7 which represents the fecundity (the number of eggs per female). Keeping $p_7 = 0$ and all other parameters except f_7 fixed with the reference values, we gradually decreased the value of f_7 from 7180.16 until the threshold value for the dominant eigenvalue approached the unity remaining above it, $\lambda_{max} > 1$. This gave us the minimal value $f_7 = 1004$ marked blue in Table 5.5. In the second test, the value for f_7 was set back to the reference, $p_7 = 0$ was kept fixed in all tests, and all other values were as in the reference except for the value of p_1 which represents the probability of surviving eggs to parr +0. Gradually decreasing the value of p_1 from 0.307 until the dominant eigenvalue was closest to unity but still larger than it, we found that the threshold value $p_1 = 0.043$ and marked it blue in the second row in Table 5.5. By repeating this process, we found the threshold values for all other parameters, $p_2 = 0.0466$, $p_3 = 0.011$, $p'_3 = 0$, $p_4 = 0$, $p_5 = 0.00393$, $p_6 = 0$, and $p'_6 = 0.00304$. These values ensure that

the dominant eigenvalue is closest to unity, but large than unity; they all are marked blue in Table 5.5.

Parameters	f_7	p_1	p_2	p_3	p'_3	p_4	p_5	p_6	p'_6	p_7
Reference	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0
Test nr. 1	1004	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0
Test nr. 2	7180.16	0.043	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0
Test nr. 3	7180.16	0.307	0.0466	0.335	0.5	0.011	0.129	0.1	0.1	0
Test nr. 4	7180.16	0.307	0.333	0.011	0.5	0.011	0.129	0.1	0.1	0
Test nr. 5	7180.16	0.307	0.333	0.335	0	0.011	0.129	0.1	0.1	0
Test nr. 6	7180.16	0.307	0.333	0.335	0.5	0	0.129	0.1	0.1	0
Test nr. 7	7180.16	0.307	0.333	0.335	0.5	0.011	0.00393	0.1	0.1	0
Test nr. 8	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0	0.1	0
Test nr. 9	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.00304	0

Table 5.5: Numerical experiment #2 consisting of nine tests.

Table 5.6 collects information from numerous tests combined into experiments; it is organized as follows. The minimal threshold values for all parameters obtained during the series of numerical tests similar to those explained in Table 5.5 and marked blue were recorded in Table 5.6. The data (marked blue and red) from Table 5.5 appear in the third row of Table 5.6 and should be interpreted as a summary of all numerical tests conducted to test the impact of the perturbation on all other parameters in the system, tested one at a time, while the remaining parameters including the red one are kept fixed. The table provides minimal threshold values for each of the parameters which guarantee that the salmon population survives if other parameters in the system are as in the reference model. The reference values for all parameters in our model are listed in the first row. All other rows represent the results of consecutive numerical experiments where several tests were performed, as explained for the experiment illustrated in Table 5.5. In some experiments, like 7, 8, 9, and 10, we fixed several parameters (marked red) to test how the model will respond to these changes.

Experiment	f_7	p_1	p_2	p_3	p'_3	p_4	p_5	p_6	p'_6	p_7
Ref.	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.05
#1	960	0.0408	0.0443	0.0076	0	0	0.00291	0	0.00226	0.05
#2	1004	0.043	0.0466	0.011	0	0	0.00393	0	0.00304	0
#3	804	0.035	0.0373	0	0	0	0	0.1	0.0127	0.2
#4	302	0.013	0.014	0	0	0	0	0	0	0.7
#5	1576	0.0674	0.0775	0.0136	0.5	0	0.00525	0	0.00406	0.05
#6	1701	0.0728	0.07891	0.01499	0.01	0	0.0058	0	0.00446	0.05
#7	3590	0.0816	0.0885	0.0577	0.5	0	0.0223	0	0.0173	0.05
#8	3590	0.1455	0.1578	0.1143	0.01	0	0.044	0	0.0341	0.05
#9	718	0.4079	0.4424	0.4591	0.5	0.043	0.1768	0.3909	0.1371	0.05
#10	718	0.7271	0.7887	0.9089	0.01	0.0858	0.35	0.7798	0.2713	0.05
#11	1063	0.0454	0.0493	0.046	0.5	0	0.0177	0.01	0.0138	0.05
#12	2078	0.0888	0.0964	0.0909	0.01	0	0.035	0.01	0.0272	0.05
#13	4733	0.2023	0.2195	0.0753	0.5	0.0043	0.029	0.0391	0.01	0.05
#14	6050	0.2586	0.2805	0.1491	0.01	0.0086	0.0575	0.078	0.01	0.05

Table 5.6: Summary of numerical experiments

Chapter 6

Conclusions and further work

What can our model tell biologists?

Many factors are important for the persistence of a species under different natural and man-affected ecologic changes. To identify these components, we conducted both sensitivity and elasticity analyses of the matrix A observing that the most significant parameters are f_7 , p_1 and p_2 , closely followed by p_3 , p_5 and p'_6 . We believe that our analysis provides an interesting insight into sustainability of the life cycle of Atlantic salmon presented schematically in Figure 5.1. We hope that low cost numerical simulations of different scenarios including so-called “worse case scenarios” where all model parameters were set to minimal values are useful for biologists. The threshold values obtained in our numerical experiments draw “red lines” signalling possible depletion of the salmon population. If field data show values close to those in Table 5.6, additional measures should be taken to prevent this. We were pleasantly surprised that the threshold values in our numerical experiments were significantly lower in comparison to reference values. This means that the nature created Atlantic salmon population with certain “safety margins” for the vital biologic parameters. Therefore, we believe that current situation allows for commercial fishing at the rates as high as 50% that does not endanger Atlantic salmon.

As a criticism of our model, we can mention that several important factors that influence the population were not considered, as in many other simple matrix models [13], including the emigration and immigration, density dependency in fertility and survival, and environmental variability. Contrary to many other biological models, we take into account only the average number of adult females and do not distinguish between fertility values for different age cohorts. It is common to assume that male and female salmon embryo are growing in the proportion 1:1, but this proportion is changing from stage to stage and these changes are not reflected in our model. Despite various deficiencies, our simple model is still useful and has substantial predictive power.

How can our model be improved?

Our simple model can be extended in several directions including more complicated relationships between salmon cohorts at different stages. For example, we can split adult cohort in several subgroups with different fertility rates. The model could be further generalized to account for the stages in saltwater, but this is rather difficult at the moment due to lack of data. We can drop the fundamental assumption that the parameters are constant. This could open the door to stochastic matrix models that incorporate random variability in parameters replacing our constant matrix A with a stochastic matrix. Another possibility is to assume that density-dependent factors influence population growth. For example, the survival rate will decrease if there is an inter-species competition for resources or an intra-species competition between males for the opportunity to mate with females. We could also include proportional harvesting into the model and explore the effect of proportional harvesting on the evolution of the population.

Table 6. Estimates of inter-stage survival (%) of Atlantic salmon in Catamaran Brook, 1990–1996.¹

Cohort	Egg to 0+ (<i>M</i>)	0+ to 1+ (<i>N</i>)	1+ to 2+ (<i>O</i>)	1+ to S2 (<i>P</i>)	2+ to S3, S4 (<i>Q</i>)	Egg to 1+ (<i>R</i>)	Egg to S (<i>S</i>)
1986							
1987					18.3		
1988			47.7	4.0	22.4		
1989		74.7	25.9	0.3	7.6		
1990	61.0	23.5	28.7	0.5	9.3	14.3	0.450
1991	24.9	32.4	42.9	1.2	12.4	8.1	0.524
1992	17.7	35.4	30.3	0.2	7.5	6.3	0.156
1993	53.9	19.8	25.5	0.3		10.7	
1994	17.3	14.0				2.4	
1995	9.2						
Average	30.7	33.3	33.5	1.1	12.9	8.4	0.376

¹0+, 1+, 2+ = parr age class; S2, S3, S4 = smolt age class; S = smolt (all age classes pooled). $M = (B+E)/A$; $N = (C+G)/(B-F)$; $O = (D+J)/(C-H)$; $P = K/(C-H)$; $Q = L/(D-J)$; $R = M \times N$; $S = (R \times P) + (R \times O \times Q)$; A to L appear in Table 5.

Figure A.2: Table 6 [12]

Table 3. Annual counts of Atlantic salmon adults (moving upstream) and smolts (moving downstream) at the fish-counting fence in Catamaran Brook, 1990–1996.

Year	Fence counts			Counts using trap efficiency		
	Smolts	Grilse	MSW	Smolts	Grilse	MSW
1990	760	83	28	1086	166	56
1991	1165	79	48	1664	88	53
1992	2135	127	67	2483	141	74
1993	426	107	44	533	113	46
1994	887	56	24	1020	56	24
1995	933	118	72	1166	131	80
1996	472	76	41	569	80	43
Average	968	92	46	1217	111	54

Figure A.3: Table 3 [12]

Appendix B

Results of our numerical experiments

In this appendix we collected the results of all fourteen numerical experiments.

They are summarized in a compact form in the Table 5.6.

Parameters	f_7	p_1	p_2	p_3	p'_3	p_4	p_5	p_6	p'_6	p_7
Reference	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.05
test nr.1	960	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.05
test nr.2	7180.16	0.0408	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.05
test nr.3	7180.16	0.307	0.0443	0.335	0.5	0.011	0.129	0.1	0.1	0.05
test nr.4	7180.16	0.307	0.333	0.0076	0.5	0.011	0.129	0.1	0.1	0.05
test nr.5	7180.16	0.307	0.333	0.335	0	0.011	0.129	0.1	0.1	0.05
test nr.6	7180.16	0.307	0.333	0.335	0.5	0	0.129	0.1	0.1	0.05
test nr.7	7180.16	0.307	0.333	0.335	0.5	0.011	0.00291	0.1	0.1	0.05
test nr.8	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0	0.1	0.05
test nr.9	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.00226	0.05

Table B.1: Numerical experiment #1.

Parameters	f_7	p_1	p_2	p_3	p'_3	p_4	p_5	p_6	p'_6	p_7
Reference	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0
test nr.1	1004	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0
test nr.2	7180.16	0.043	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0
test nr.3	7180.16	0.307	0.0466	0.335	0.5	0.011	0.129	0.1	0.1	0
test nr.4	7180.16	0.307	0.333	0.011	0.5	0.011	0.129	0.1	0.1	0
test nr.5	7180.16	0.307	0.333	0.335	0	0.011	0.129	0.1	0.1	0
test nr.6	7180.16	0.307	0.333	0.335	0.5	0	0.129	0.1	0.1	0
test nr.7	7180.16	0.307	0.333	0.335	0.5	0.011	0.00393	0.1	0.1	0
test nr.8	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0	0.1	0
test nr.9	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.00304	0

Table B.2: Numerical experiment #2.

Parameters	f7	p1	p2	p3	p3'	p4	p5	p6	p6'	p7
Reference	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.2
test nr.1	804	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.2
test nr.2	7180.16	0.035	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.2
test nr.3	7180.16	0.307	0.0373	0.335	0.5	0.011	0.129	0.1	0.1	0.2
test nr.4	7180.16	0.307	0.333	0	0.5	0.011	0.129	0.1	0.1	0.2
test nr.5	7180.16	0.307	0.333	0.335	0	0.011	0.129	0.1	0.1	0.2
test nr.6	7180.16	0.307	0.333	0.335	0.5	0	0.129	0.1	0.1	0.2
test nr.7	7180.16	0.307	0.333	0.335	0.5	0.011	0	0.1	0.1	0.2
test nr.8	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0	0.1	0.2
test nr.9	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.0127	0.2
test nr.10	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.2

Table B.3: Numerical experiment #3.

Parameters	f7	p1	p2	p3	p3'	p4	p5	p6	p6'	p7
Reference	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.7
test nr.1	302	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.7
test nr.2	7180.16	0.013	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.7
test nr.3	7180.16	0.307	0.014	0.335	0.5	0.011	0.129	0.1	0.1	0.7
test nr.4	7180.16	0.307	0.333	0	0.5	0.011	0.129	0.1	0.1	0.7
test nr.5	7180.16	0.307	0.333	0.335	0	0.011	0.129	0.1	0.1	0.7
test nr.6	7180.16	0.307	0.333	0.335	0.5	0	0.129	0.1	0.1	0.7
test nr.7	7180.16	0.307	0.333	0.335	0.5	0.011	0	0.1	0.1	0.7
test nr.8	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.7
test nr.9	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.00473	0.7

Table B.4: Numerical experiment #4.

Parameters	f7	p1	p2	p3	p3'	p4	p5	p6	p6'	p7
Reference	7180.16	0.307	0.333	0.335	0.1	0.011	0.129	0.1	0.1	0.05
test nr.1	1576	0.307	0.333	0.335	0.1	0.011	0.129	0.1	0.1	0.05
test nr.2	7180.16	0.0674	0.333	0.335	0.1	0.011	0.129	0.1	0.1	0.05
test nr.3	7180.16	0.307	0.0775	0.335	0.1	0.011	0.129	0.1	0.1	0.05
test nr.4	7180.16	0.307	0.333	0.0136	0.1	0.011	0.129	0.1	0.1	0.05
test nr.5	7180.16	0.307	0.333	0.335	0.1	0.011	0.129	0.1	0.1	0.05
test nr.6	7180.16	0.307	0.333	0.335	0.1	0	0.129	0.1	0.1	0.05
test nr.7	7180.16	0.307	0.333	0.335	0.1	0.011	0.00525	0.1	0.1	0.05
test nr.8	7180.16	0.307	0.333	0.335	0.1	0.011	0.129	0	0.1	0.05
test nr.9	7180.16	0.307	0.333	0.335	0.1	0.011	0.129	0.1	0.00406	0.05

Table B.5: Numerical experiment #5.

Parameters	f7	p1	p2	p3	p3'	p4	p5	p6	p6'	p7
Reference	7180.16	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.1	0.05
test nr.1	1701	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.1	0.05
test nr.2	7180.16	0.0728	0.333	0.335	0.01	0.011	0.129	0.1	0.1	0.05
test nr.3	7180.16	0.307	0.07891	0.335	0.01	0.011	0.129	0.1	0.1	0.05
test nr.4	7180.16	0.307	0.333	0.01499	0.01	0.011	0.129	0.1	0.1	0.05
test nr.5	7180.16	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.1	0.05
test nr.6	7180.16	0.307	0.333	0.335	0.01	0	0.129	0.1	0.1	0.05
test nr.7	7180.16	0.307	0.333	0.335	0.01	0.011	0.0058	0.1	0.1	0.05
test nr.8	7180.16	0.307	0.333	0.335	0.01	0.011	0.129	0	0.1	0.05
test nr.9	7180.16	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.00406	0.05

Table B.6: Numerical experiment #6.

Parameters	f7	p1	p2	p3	p3'	p4	p5	p6	p6'	p7
Reference	7180.16	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.05
test nr.1	1701	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.05
test nr.2	3590	0.0816	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.05
test nr.3	3590	0.307	0.0885	0.335	0.5	0.011	0.129	0.1	0.1	0.05
test nr.4	3590	0.307	0.333	0.0577	0.5	0.011	0.129	0.1	0.1	0.05
test nr.5	3590	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.05
test nr.6	3590	0.307	0.333	0.335	0.5	0	0.129	0.1	0.1	0.05
test nr.7	3590	0.307	0.333	0.335	0.5	0.011	0.0223	0.1	0.1	0.05
test nr.8	3590	0.307	0.333	0.335	0.5	0.011	0.129	0	0.1	0.05
test nr.9	3590	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.0173	0.05

Table B.7: Numerical experiment #7.

Parameters	f7	p1	p2	p3	p3'	p4	p5	p6	p6'	p7
Reference	3590	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.1	0.05
test nr.1	1701	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.1	0.05
test nr.2	3590	0.1455	0.333	0.335	0.01	0.011	0.129	0.1	0.1	0.05
test nr.3	3590	0.307	0.1578	0.335	0.01	0.011	0.129	0.1	0.1	0.05
test nr.4	3590	0.307	0.333	0.1143	0.01	0.011	0.129	0.1	0.1	0.05
test nr.5	3590	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.1	0.05
test nr.6	3590	0.307	0.333	0.335	0.01	0	0.129	0.1	0.1	0.05
test nr.7	3590	0.307	0.333	0.335	0.01	0.011	0.044	0.1	0.1	0.05
test nr.8	3590	0.307	0.333	0.335	0.01	0.011	0.129	0	0.1	0.05
test nr.9	3590	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.0341	0.05

Table B.8: Numerical experiment #8.

Parameters	f7	p1	p2	p3	p3'	p4	p5	p6	p6'	p7
Reference	718	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.05
test nr.1	718	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.05
test nr.2	718	0.4079	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.05
test nr.3	718	0.307	0.4424	0.335	0.5	0.011	0.129	0.1	0.1	0.05
test nr.4	718	0.307	0.333	0.4591	0.5	0.011	0.129	0.1	0.1	0.05
test nr.5	718	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1	0.05
test nr.6	718	0.307	0.333	0.335	0.5	0.043	0.129	0.1	0.1	0.05
test nr.7	718	0.307	0.333	0.335	0.5	0.011	0.1768	0.1	0.1	0.05
test nr.8	718	0.307	0.333	0.335	0.5	0.011	0.129	0.3909	0.1	0.05
test nr.9	718	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.1371	0.05

Table B.9: Numerical experiment #9.

Parameters	f7	p1	p2	p3	p3'	p4	p5	p6	p6'	p7
Reference	718	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.1	0.05
test nr.1	718	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.1	0.05
test nr.2	718	0.7271	0.333	0.335	0.01	0.011	0.129	0.1	0.1	0.05
test nr.3	718	0.307	0.7887	0.335	0.01	0.011	0.129	0.1	0.1	0.05
test nr.4	718	0.307	0.333	0.9089	0.01	0.011	0.129	0.1	0.1	0.05
test nr.5	718	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.1	0.05
test nr.6	718	0.307	0.333	0.335	0.01	0.0858	0.129	0.1	0.1	0.05
test nr.7	718	0.307	0.333	0.335	0.01	0.011	0.35	0.1	0.1	0.05
test nr.8	718	0.307	0.333	0.335	0.01	0.011	0.129	0.7798	0.1	0.05
test nr.9	718	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.2713	0.05

Table B.10: Numerical experiment #10.

Parameters	f7	p1	p2	p3	p3'	p4	p5	p6	p6'	p7
Reference	7180	0.307	0.333	0.335	0.5	0.011	0.129	0.01	0.1	0.05
test nr.1	1063	0.307	0.333	0.335	0.5	0.011	0.129	0.01	0.1	0.05
test nr.2	7180	0.0454	0.333	0.335	0.5	0.011	0.129	0.01	0.1	0.05
test nr.3	7180	0.307	0.0493	0.335	0.5	0.011	0.129	0.01	0.1	0.05
test nr.4	7180	0.307	0.333	0.046	0.5	0.011	0.129	0.01	0.1	0.05
test nr.5	7180	0.307	0.333	0.335	0.5	0.011	0.129	0.01	0.1	0.05
test nr.6	7180	0.307	0.333	0.335	0.5	0	0.129	0.01	0.1	0.05
test nr.7	7180	0.307	0.333	0.335	0.5	0.011	0.0177	0.01	0.1	0.05
test nr.8	7180	0.307	0.333	0.335	0.5	0.011	0.129	0.01	0.1	0.05
test nr.9	7180	0.307	0.333	0.335	0.5	0.011	0.129	0.01	0.0138	0.05

Table B.11: Numerical experiment # 11.

Parameters	f7	p1	p2	p3	p3'	p4	p5	p6	p6'	p7
Reference	7180	0.307	0.333	0.335	0.5	0.011	0.129	0.01	0.1	0.05
test nr.1	2078	0.307	0.333	0.335	0.5	0.011	0.129	0.01	0.1	0.05
test nr.2	7180	0.0888	0.333	0.335	0.5	0.011	0.129	0.01	0.1	0.05
test nr.3	7180	0.307	0.0964	0.335	0.5	0.011	0.129	0.01	0.1	0.05
test nr.4	7180	0.307	0.333	0.0909	0.5	0.011	0.129	0.01	0.1	0.05
test nr.5	7180	0.307	0.333	0.335	0.5	0.011	0.129	0.01	0.1	0.05
test nr.6	7180	0.307	0.333	0.335	0.5	0	0.129	0.01	0.1	0.05
test nr.7	7180	0.307	0.333	0.335	0.5	0.011	0.035	0.01	0.1	0.05
test nr.8	7180	0.307	0.333	0.335	0.5	0.011	0.129	0.01	0.1	0.05
test nr.9	7180	0.307	0.333	0.335	0.5	0.011	0.129	0.01	0.0272	0.05

Table B.12: Numerical experiment #12.

Parameters	f7	p1	p2	p3	p3'	p4	p5	p6	p6'	p7
Reference	7180	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.01	0.05
test nr.1	4733	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.01	0.05
test nr.2	7180	0.2023	0.333	0.335	0.5	0.011	0.129	0.1	0.01	0.05
test nr.3	7180	0.307	0.2195	0.335	0.5	0.011	0.129	0.1	0.01	0.05
test nr.4	7180	0.307	0.333	0.0753	0.5	0.011	0.129	0.1	0.01	0.05
test nr.5	7180	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.01	0.05
test nr.6	7180	0.307	0.333	0.335	0.5	0.0043	0.129	0.1	0.01	0.05
test nr.7	7180	0.307	0.333	0.335	0.5	0.011	0.029	0.1	0.01	0.05
test nr.8	7180	0.307	0.333	0.335	0.5	0.011	0.129	0.0391	0.01	0.05
test nr.9	7180	0.307	0.333	0.335	0.5	0.011	0.129	0.1	0.01	0.05

Table B.13: Numerical experiment #13.

Parameters	f7	p1	p2	p3	p3'	p4	p5	p6	p6'	p7
Reference	7180	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.01	0.05
test nr.1	6050	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.01	0.05
test nr.2	7180	0.2586	0.333	0.335	0.01	0.011	0.129	0.1	0.01	0.05
test nr.3	7180	0.307	0.2805	0.335	0.01	0.011	0.129	0.1	0.01	0.05
test nr.4	7180	0.307	0.333	0.1491	0.01	0.011	0.129	0.1	0.01	0.05
test nr.5	7180	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.01	0.05
test nr.6	7180	0.307	0.333	0.335	0.01	0.0086	0.129	0.1	0.01	0.05
test nr.7	7180	0.307	0.333	0.335	0.01	0.011	0.0575	0.1	0.01	0.05
test nr.8	7180	0.307	0.333	0.335	0.01	0.011	0.129	0.078	0.01	0.05
test nr.9	7180	0.307	0.333	0.335	0.01	0.011	0.129	0.1	0.01	0.05

Table B.14: Numerical experiment #14.

Appendix C

Matlab codes

In this appendix we included Matlab codes used for running numerical experiments.

C.1 Tests for finding the closest to unity value of the dominant eigenvalue

```
1 % To calculate the minimum value that gives us the
   eigenvalue of the matrix larger than 1.
2 %Here v is the target parameter that we test.
3
4 function [c,q]=z()
5 q=0;
6 c=0;
7 for i=1:10000
8     if i==1
9         v=0;
10    else
11        v=(i-1)/10000;
12    end
13 row1=[0 0 0 0 0 0 7180 ];
```

```

14 row2=[v 0 0 0 0 0 0 ];
15 row3=[0 0.333 0 0 0 0 0 ];
16 row4=[0 0 0.335 0.5 0 0 0 ];
17 row5=[0 0 0.011 0 0 0 0 ];
18 row6=[0 0 0 0.129 0 0 0 ];
19 row7=[0 0 0 0 0.1 0.1 0.05 ];
20 A=[row1;row2;row3;row4;row5;row6;row7];
21 V=eig(A);
22 if real(V(1,1))>1
23     q=V(1,1);
24     c=(i-1)/10000;
25     return;
26 elseif real(V(2,1))>1
27     q=V(2,1);
28     c=(i-1)/10000;
29     return;
30 elseif real(V(3,1))>1
31     q=V(3,1);
32     c=(i-1)/10000;
33     return;
34 elseif real(V(4,1))>1
35     q=V(4,1);
36     c=(i-1)/10000;
37     return;
38 elseif real(V(5,1))>1
39     q=V(5,1);
40     c=(i-1)/10000;
41     return;
42 elseif real(V(6,1))>1
43     q=V(6,1);

```



```

44     c=(i-1)/10000;
45     return;
46 elseif real(V(7,1))>1
47     q=V(7,1);
48     c=(i-1)/10000;
49     return;
50 else
51     continue
52 end
53 end

```

C.2 Calculation of the sensitivity and elasticity

```

1 %To calculate the sensitivity and elasticity of the
   dominant eigenvalue.
2
3     function [m]=s ()
4 n=7;
5 row1=[0 0 0 0 0 0 7180.16];
6 row2=[0.307 0 0 0 0 0 0];
7 row3=[0 0.333 0 0 0 0 0];
8 row4=[0 0 0.335 0.5 0 0 0];
9 row5=[0 0 0.011 0 0 0 0];
10 row6=[0 0 0 0.129 0 0 0];
11 row7=[0 0 0 0 0.1 0.1 0.05];
12 A=[row1;row2;row3;row4;row5;row6;row7];
13 [W,D,V]=eig(A);
14 g=max(D, [], 'all');
15 q=0;
16 for i=1:7

```

```

17     if D(i , i)==g
18         q=i ;
19     end
20 end
21 c=0;
22 m=zeros(n,n);
23 Q=V(:,q);
24 P=W(:,q);
25 c=transpose(P)*Q;
26 for i=1:7
27     for j=1:7
28         % m(i,j)=(Q(i,1)*P(j,1))/c; % Here is the part to
                calculate the sensitivity.
29         m(i,j)=(A(i,j)*Q(i,1)*P(j,1))/(c*g); %The part to
                calculate the elasticity.
30     end
31 end
32 g
33 for i=1:7
34     for j=1:7
35         if A(i,j)==0
36             m(i,j)=0;
37         end
38     end
39 end
40 end

```

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