ELUCIDATING THE DECLINE OF NORTH AMERICAN ATLANTIC SALMON WITH A TIME-DEPENDENT MATRIX MODEL

by

Rui Zhang

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To my beloved wife

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ABSTRACT

North American Atlantic salmon populations have declined significantly since the 1990s, especially the elder life stages. The total average number of returned two-sea-winter (2SW) in the period 1997 to 2007 dropped by 57% compared to that in the period 1972 to 1982. Evidence is emerging that the decline is largely due to poor marine survival. Since the marine phase of the salmon life cycle lasts several years and spans a large geographic range, it remains unclear at which specific life stage the most significant decline occurs. To address this question, I developed a new method to assess the status and fluctuations of the North American Atlantic salmon population. By applying an optimization algorithm to fit an age- and stage-structured matrix model to available observations for the period from 1972 to 2011, I assess stage-specific mortality rates over time. The model is able to closely replicate the observations and provides insights into the temporal variation of one-sea-winter (1SW) and two-sea-winter (2SW) salmon returns. Results suggest that changes in the relative proportion of the 1SW and 2SW returns resulted from a 28% decrease of survival during the second year at sea since 1992. By combining model outputs, and homewater and distant fishery catch data, I quantified the relative influence of bottom-up (i.e., environmental changes) and top-down effects (i.e., fishing pressure). It shows the environmental impact has a generally negative effect on Atlantic salmon survival, with a 41% decrease near West Greenland during the second year at sea and a 17% decrease near Canadian homewater during migration to their spawning grounds since 1992. In addition to the importance of external environmental change impacting the population dynamics of North American Atlantic salmon, I show that the moratorium on commercial fishing is likely insufficient for recovery of Atlantic salmon to previous abundance levels. However, the moratorium is crucial, at least in the short term, to maintain the relatively low yet stable abundance of Atlantic salmon.

List of Abbreviations Used

Abbreviations	Description
1SW	One-sea-winter; salmon that spend one winter at sea before they mature
2SW	Two-sea-winter; salmon that spend two winters at sea before they mature
3SW	Three-sea-winter; salmon that spend three winters at sea before they mature
SST	Sea surface temperature
NAO	North Atlantic Oscillation index
AMO	Atlantic Multidecadal Oscillation index
PFA	Pre-fishery abundance
ICES	International Council for the Exploration of the Sea
NASCO	North Atlantic Salmon Conservation Organization
PDF	Probability density function
RMSD	Root mean square deviation

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Chapter 1

Introduction

Atlantic salmon (*Salmo salar L.*) is an anadromous fish species with a complex life-history that encompasses their hatching and initial juvenile growth in freshwater, smoltification, followed by a migration to productive marine feeding grounds, and a return migration to their natal river for spawning (Asa et al., 2011). The North American Atlantic salmon populations span a broad geographic range that historically extended from Ungava Bay, Canada, to Long Island Sound, United States of America (Figure 1.1). Atlantic salmon that spend more than one winter in the ocean undertake wide-ranging migrations to common feeding grounds off West Greenland and in the Labrador Sea (Thorstad et al., 2011), during which they are exposed to a range of environmental conditions.

Declines in North American Atlantic salmon populations have been observed in recent decades, especially in their southernmost reaches (i.e., Gulf of Maine, Bay of Fundy and Scotian Shelf) and among fish maturing after two winters at sea (two sea-winter salmon, or 2SW) (Parrish et al., 1998; ICES 2015; Figure 1.2). The populations from Quebec, the Gulf of St Lawrence and the Scotian Shelf dominate the total North American Atlantic salmon population, and all three show a declining trend over the period 1972 to 2007. Populations from Labrador and Newfoundland make up a relatively small fraction of the total population over the period 1972 to 1992 and have increased since 1992, which represents a positive response to the 1992 closure of the commercial salmon and cod fisheries.

The commercial fishery is an obvious and significant factor impacting the salmon population. The Government of Canada imposed a moratorium on the commercial salmon fishery for the Maritime provinces in 1984 and for the Newfoundland and Labrador salmon fishery in 1992, which together with the closure of the northern cod fishery (also in 1992), reduced the by-catch of salmon considerably (Federation 1994). The Greenland fishery was the largest commercial salmon fishery in the world around the 1960s and it was not until the early 1980s that quotas on the salmon fisheries were agreed to and began to result in reduced catches. Since 1995, the West Greenland fishery has been severely restricted due to a quota agreed to by North Atlantic Salmon Conservation Organization (NASCO) based on pre-fishery abundance advice from International Council for the Exploration of the Sea (ICES).

Despite substantial efforts to reduce fishing pressure and protect freshwater habitats, Atlantic salmon stocks have shown little evidence of recovery from 1990 to 2010 (Frank et al. 2011). Unlike during the early life stages in freshwater, salmon in their marine environment are challenged by multiple physiological stressors and exposed to a wide array of predators, which makes survival rates variable (Thorstad et al. 2011; Chaput 2012). Recent studies suggest a decrease survival in response to warmer marine temperatures and bottom-up control effects (i.e., changes in physical conditions leading to a decrease of plankton abundance and prey availability for salmon) driven by climate change (Beaugrand and Reid, 2012; Chaput and Benoit, 2012; Friedland et al., 2013; Mills et al., 2013). The above studies include Atlantic salmon populations from both North American and European continents. For example, Friedland et al. (2012) examined sea surface temperature (SST), chlorophyll, net primary production and zooplankton related to the weight of salmon based on a correlation analysis and found that salmon growth was highly associated with the thermal regime during winter and spring, with correlation significant at $P = 0.01$ or $P = 0.05$. Beaugrand et al. (2012) determined correlations between SST and growth, survival and maturation of salmon during marine migrations. Mills et al. (2013) suggested climate conditions represented by the North Atlantic Oscillation (NAO) and the Atlantic Multi-decadal Oscillation (AMO) meteorological indexes are associated with changes in plankton communities and prey availability (e.g., 55% correlation between capelin and AMO), which are ultimately linked to Atlantic salmon populations. However, since most of the studies are based on correlation or cluster analysis, a better mechanistic understanding of climate-driven effects propagating through the food web and their impacts on different life stages of salmon is needed.

To manage distant water fisheries (i.e., salmon near West Greenland and the Faroe

Islands), the International Council for the Exploration of the Sea (ICES) developed a model to forecast Atlantic salmon abundance prior to any fisheries removals: The Pre-Fishery Abundance (hereafter denoted as PFA). The basic input data to their model are annual returns of 1SW and 2SW salmon, which are used to estimate the maturing and non-maturing components of PFA. The maturing component returns after one winter spent at sea and the non-maturing component remains at sea for at least one extra winter before migrating to spawning grounds. The ICES model assumes that natural mortality at sea between PFA and returned salmon is constant over time (Rago et al., 1993; Chaput, 2012). This implicitly assumes that changes in the relative proportion of 1SW and 2SW salmon returns result from changes in the proportion of maturing PFA and not in the survival rate at sea, which is highly unlikely (Chaput, 2012). Moreover, complex life history of Atlantic salmon is coarsely represented in the model. The lack of separation of different life stages make it difficult to incorporate available data to improve model performance.

In this study, I developed a new method to assess the North American Atlantic salmon stock by applying an optimization algorithm to fit an age- and stage-structured matrix model to the available observation data (i.e., returns of 1SW and 2SW). Matrix models, introduced by Leslie (1945), are powerful tools for population dynamic studies (Caswell, 2001). They are based on biological fundamentals (i.e., recruitment, aging and survival, etc.) and allow flexibility in simulating complex dynamic behaviour. Existing data can be used in a matrix model that incorporates all life stages and key stages where additional data required can be identified (Browne 1988). Simulation also provides a method of investigating the effects of proposed management options by estimating future projections. For example, Horst (1988) used a Leslie model to evaluate how changes in mortality in different life stages could influence population growth rate of cunner, and showed that changes in survival rate at young ages resulted in the greatest effect on the population growth rate. Kareiva et al. (2000) applied a matrix model to assess effects of dams on Chinook salmon in the Columbia River Basin and concluded that dam removal would not reverse the decline of Chinook salmon. Lundqvist et al. (2008) evaluated effects of hydropower development by increasing the return probability on the salmon population size in a regulated river in Sweden and predicted the future population trend. Ferguson et al. (2008) combined turbine blade-strike estimates and matrix models to assess mitigation strategies for fish passing dams.

However, such models require precisely estimated parameters, and for Atlantic salmon, the abundance data of the marine phase and information on life history parameters are often limited. To solve this problem, I applied an optimization algorithm to systematically tune model parameters until the misfit between model and observations is minimized. This approach assumes that the unobserved phases of the population can be derived from the observed phases given the constraints imposed by the population model. Optimization techniques are often applied to marine biogeochemical models (e.g., Friedrichs et al., 2007; Bagniewski et al., 2011; Wilson et al., 2013; Kuhn et al., 2015). In this study, given the available knowledge of the Atlantic salmon life cycle and the available observations (i.e., returns of 1SW and 2SW salmon), I aim to reconstruct the best representation of the hidden marine phase. By dividing the entire simulation period into time segments, I am able to produce time-dependent parameters, investigate their temporal variations and demonstrate which life stages are important in explaining the population decline. Additionally, I quantify the relative influence of fishing pressure and environmental conditions on various salmon life-history stages and the stock. Finally, I compare the matrix model results with PFA from ICES's model. Implications for future fishery management are also addressed in Chapter 4.

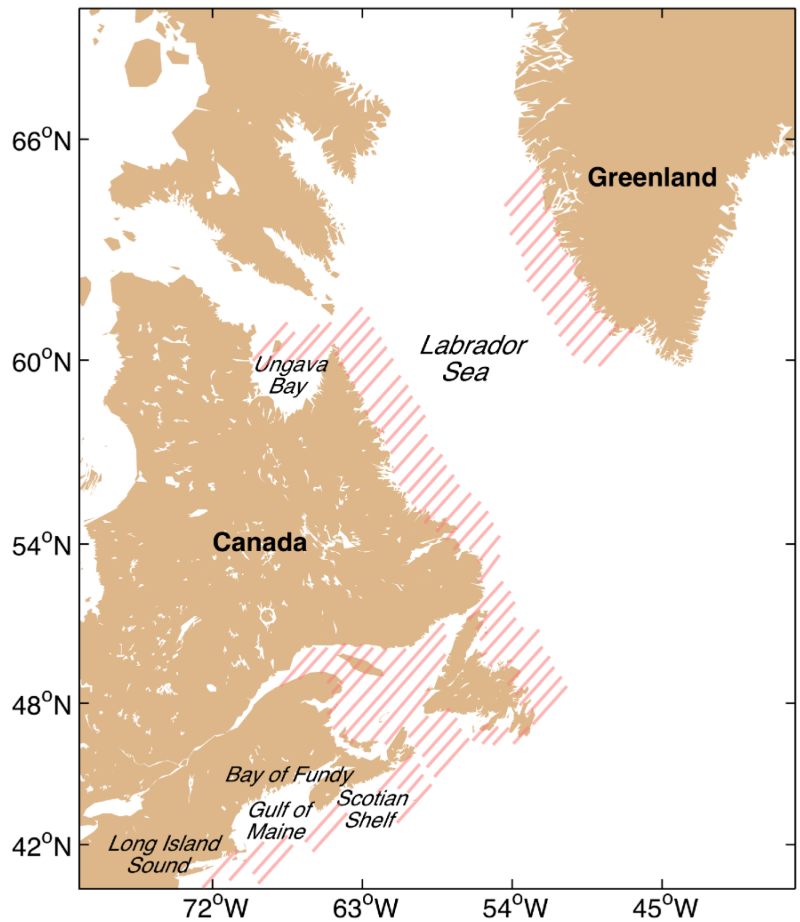

Figure 1.1: Geographic range of North American Atlantic salmon, as indicated by shaded area

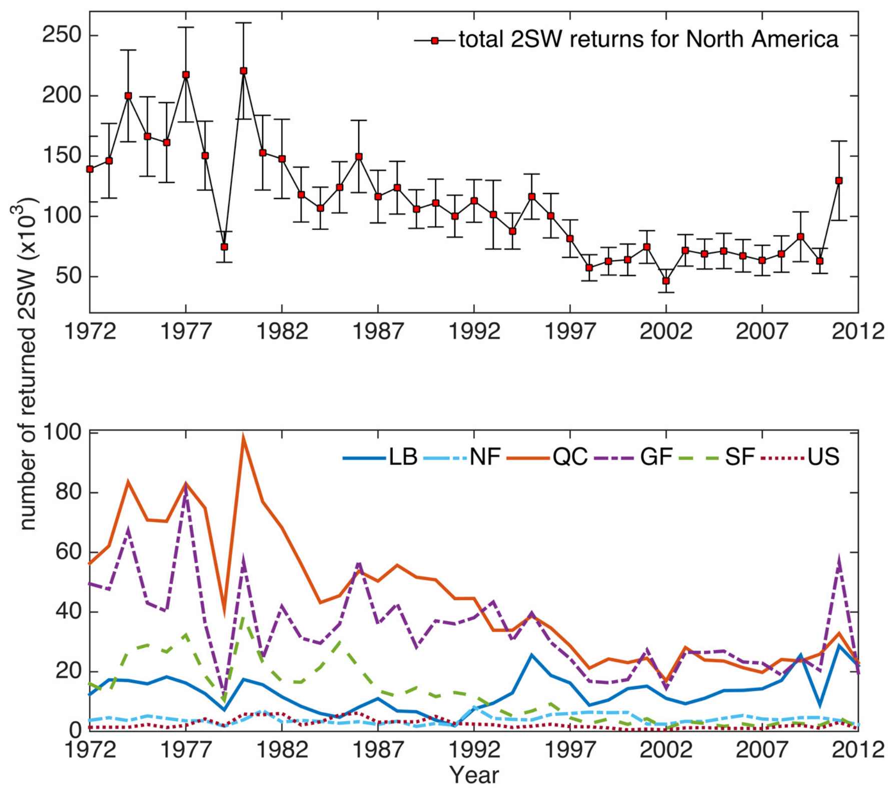

Figure 1.2: Total returns of 2SW for North America (top panel) and for each of six regions (Labrador-LB, Newfoundland-NF, Quebec-QC, Gulf of St Lawrence-GF, Scotian Shelf-SF and U.S.-US; bottom panel; ICES 2015)

CHAPTER 2

METHODS

2.1 Leslie model

Before describing the specific matrix model for Atlantic salmon, I present a general introduction to the Leslie model (Leslie, 1945) by illustrating several ideal cases using a population with three life stages. I assume a species with three age classes (i.e., juveniles, subadults and adults) and an initial population with 1000 females in each of the three age classes. The survival probabilities for the first and second age classes are given by P1 and P2 and fecundities for the second and third age classes are given by F1 and F2. The following matrix equation describes how the population evolves over the course of one-time step:

$$\begin{pmatrix} n_1 \\ n_2 \\ n_3 \end{pmatrix}_{t+1} = \begin{pmatrix} 0 & F1 & F2 \\ P1 & 0 & 0 \\ 0 & P2 & 0 \end{pmatrix} \times \begin{pmatrix} n_1 \\ n_2 \\ n_3 \end{pmatrix}_{t} \tag{2.1}$$

It can be written in a more compact form:

$$n(t+1) = Mn(t) \tag{2.2}$$

where $n(t)$ is the population vector containing the number of individuals in each age or stage class at time t, and M is the so-called projection matrix. Parameters of survival probabilities and fecundities are certainly affected by external environmental factors and can vary temporally. However, here we begin with the simplest idealized situation assuming all the parameters are constant. An investigation of the eigenvalues of the projection matrix can reveal a great deal of the resulting population dynamics (Caswell, 2001), and is independent of the initial population vector. I assume matrix A has three distinct eigenvalues λ_1, λ_2 and λ_3, and three linearly independent eigenvectors v_1, v_2 and v_3 such that

$$Mv_i = \lambda_i v_i \tag{2.3}$$

After some algebraic manipulation, (2.3) can be written as:

$$n(t) = \sum_i c_i \lambda_i^t v_i \tag{2.4}$$

where c_i are coefficients related to the initial vector, which shows that the long-term behaviour of $n(t)$ is determined by the eigenvalues λ_i as they are raised to higher and higher powers. (2.4) decomposes the growth of a stage-structured population into a set of exponential contributions, one for each eigenvalue.

Several cases can be distinguished. If λ_i is real, then
if $\lambda_i > 1$, λ_i^t increases exponentially,
if $\lambda_i = 1$, λ_i^t is stable,
if $0 < \lambda_i < 1$, λ_i^t decreases exponentially,
if $-1 < \lambda_i < 0$, λ_i^t exhibits damped oscillations,
if $\lambda_i = -1$, λ_i^t exhibits undamped oscillations,
if $\lambda_i < -1$, λ_i^t exhibits diverging oscillations.
If λ_i is complex, λ_i^t exhibits damped oscillations when $|\lambda_i| < 1$ and diverging oscillations when $|\lambda_i| > 1$.

Dividing both sides (2.4) by λ_1^t yields

$$\frac{n(t)}{\lambda_1^t} = c_1 v_1 + c_2 (\frac{\lambda_2}{\lambda_1})^t + c_3 (\frac{\lambda_3}{\lambda_1})^t + \dots \tag{2.5}$$

since $\lambda_1 > |\lambda_2|$ (assuming λ_1 is the dominant eigenvalue),

$$\lim_{t \to \infty} \frac{n(t)}{\lambda_1^t} = c_1 v_1 \tag{2.6}$$

which means, regardless of the initial population, the other exponential terms will eventually become negligible and the population will grow at a rate given by the dominant eigenvalue λ_1 and converge to an age structure proportional to the dominant eigenvector v_1. From (2.5) the convergence to the stable age distribution will be more rapid the larger λ_1 is relative to the other eigenvalues. The rate of convergence is determined by the ratio of the largest to second large eigenvalue, which is defined as the damping ratio:

$$d = \frac{\lambda_1}{|\lambda_2|} \tag{2.7}$$

In the simple case of three age groups, 6 different scenarios can provide a simulation of the population dynamics over 25 years (Table 2.1). For experiments 1, 2 and 3, I assume F1 equals 0; all reproduction is concentrated in the last age class and assumes different survival rates and fecundities for each scenario. For experiments 4, 5 and 6, I assign positive values to both F1 and F2. All eigenvalues λ_i, their magnitude $|\lambda_i|$ and the damping ratio are calculated.

Table 2.1: Setup of 6 scenarios with 3 by 3 projection matrix

Exp	Matrix	Eigenvalues(λ_i)	Magnitude($\lvert\lambda_i\rvert$)	Damping ratio
1	$\begin{pmatrix} 0 & 0 & 2000 \\ 0.05 & 0 & 0 \\ 0 & 0.10 & 0 \end{pmatrix}$	2.15	2.15	1.00
		-1.08+1.87i	2.15	
		-1.08 -1.87i	2.15	
2	$\begin{pmatrix} 0 & 0 & 1608 \\ 0.03 & 0 & 0 \\ 0 & 0.02 & 0 \end{pmatrix}$	1.00	1.00	1.00
		-0.50+0.87i	1.00	
		-0.50 -0.87i	1.00	
3	$\begin{pmatrix} 0 & 0 & 1000 \\ 0.02 & 0 & 0 \\ 0 & 0.02 & 0 \end{pmatrix}$	0.74	0.74	1.00
		-0.37+0.64i	0.74	
		-0.37 -0.64i	0.74	
4	$\begin{pmatrix} 0 & 300 & 2000 \\ 0.05 & 0 & 0 \\ 0 & 0.10 & 0 \end{pmatrix}$	4.17	4.17	1.20
		3.48	3.48	
		0.69	0.69	
5	$\begin{pmatrix} 0 & 30 & 1000 \\ 0.02 & 0 & 0 \\ 0 & 0.02 & 0 \end{pmatrix}$	1.00	1.00	1.58
		-0.50+0.39i	0.63	
		-0.50 -0.39i	0.63	
6	$\begin{pmatrix} 0 & 20 & 500 \\ 0.01 & 0 & 0 \\ 0 & 0.02 & 0 \end{pmatrix}$	0.60	0.60	1.49
		-0.30+0.27i	0.41	
		-0.30 -0.27i	0.41	

When the fecundity is limited to only one age group, the age structure oscillates with a certain period of 3 years (experiments 1, 2 and 3 in Table 2.1 and Figure 2.1). In contrast, the age structure will converge when the fecundity is not limited to one age group

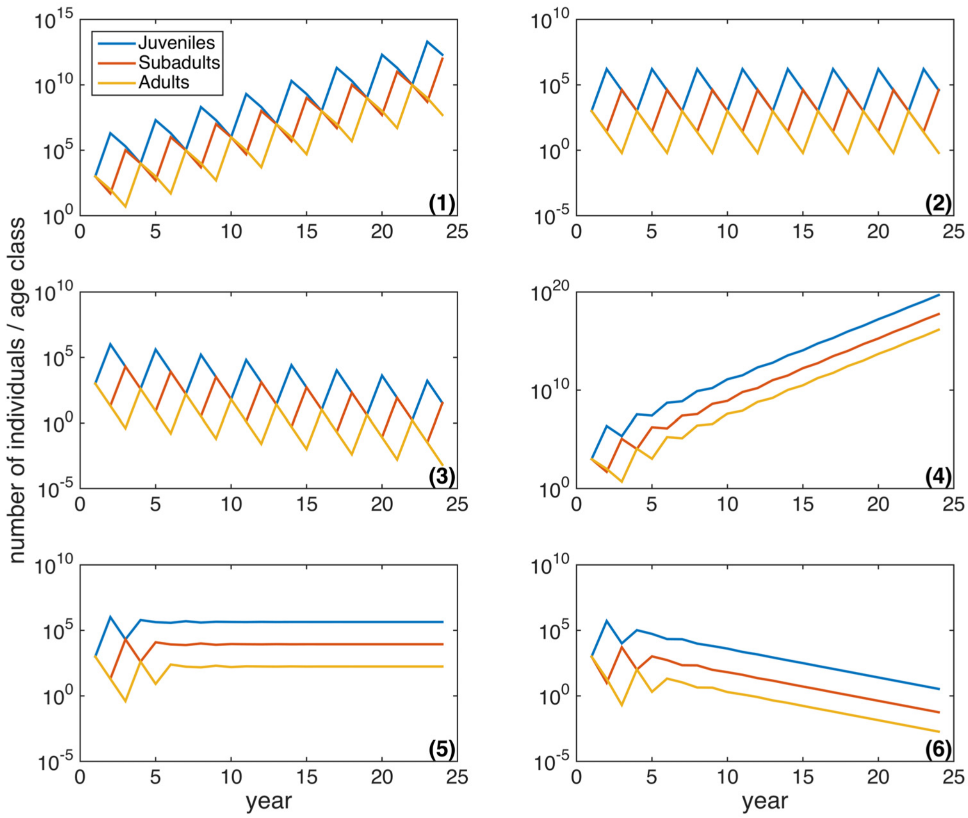

Figure 2.1: Simulated results using the project matrix of Table 2.1, six panels corresponds with six experiments. Blue, red and yellow lines represents evolution of number of individuals for juvenile, subadult and adult age groups.

(experiments 4, 5 and 6 in Table 2.1 and Figure 2.1). The population trend of oscillation or convergence can be explained by the damping ratio. In experiments 1, 2 and 3 all eigenvalues share the same magnitude and thus the damping ratio always equals 1. In experiments 4, 5 and 6 the damping ratio doesn't equal 1 anymore. The experiments also illustrate how the magnitude of the dominant eigenvalue governs the trend of the population, i.e., whether the population will increase (experiments 1 and 4), remain stable (experiments 2 and 5) or decrease (experiments 3 and 6) when λ_1 is larger, equal or smaller than 1. Showing the idealized cases, I demonstrate the ability of the matrix model to capture the trend, oscillation and convergence rate, but also show that an idealized model lacking temporal variation of parameters cannot resolve complex variability of the population dynamics.

2.2 Atlantic salmon model

For the study of Atlantic salmon, I developed a Leslie matrix model that incorporates the major life-history stages and different maturation phenotypes: egg, smolt, 1SW, 2SW, 3SW salmon and repeat spawners, as illustrated in Figure 2.2. I included two freshwater phases (egg and smolt) and four maturation phenotypes at sea based on the number of winters they spend in the ocean. These alternative maturation phenotypes are present in most Atlantic salmon populations. For simplicity, I ignore salmon maturing in freshwater as parr (i.e., juvenile phase of salmon between egg and smolt) and salmon that spend more than three winters at sea. I assumed repeat spawners only spawn twice, and a 50:50 sex ratio. I also ignore individual growth rate, the effects of density on survival and age-specific partitioning of the freshwater phase.

The model introduces eggs and smolts as juvenile phases in freshwater. Survival probabilities describing egg to smolt and smolt to 1SW salmon (first year at sea) are given by P1 and P2. Different maturation strategies are included within the model and are represented by parameters representing the proportion of post-smolts that mature to return as spawners at a given age (Pr1, Pr2, Pr3 and Prk for 1SW, 2SW, 3SW and repeat spawners, respectively). The term (1-Pr) then represents the proportion that stay at sea for at least one more winter before migrating to spawning grounds. Pr increases with older age classes. I assume that returning salmon of different age groups have the same survival probability as Pm during their riverward migration. Salmon that mature later are subject to survival probabilities for their additional years at sea (P3 and P4). Considering the paucity of data on survival probabilities during the spawning migration, the same survival probability for all age groups during riverward migration (Pm) was assumed. A change in Pr over time reflects a modification in the species' maturation schedule, while changes in P3, P4 and Pm reflect variations in survival rate as a response to both fishing pressure and environmental conditions. Thus, the product of probabilities Pr1·Pm describes survival rate from first year at sea salmon to returned 1SW salmon, and (1-Pr1)·P3 describes the survival rate from first year at sea salmon to the second year at sea salmon. The same pattern applies to the following age groups as well. Returned 1SW, 2SW and 3SW salmon have the same survival probability as repeat spawners, given by Pk.

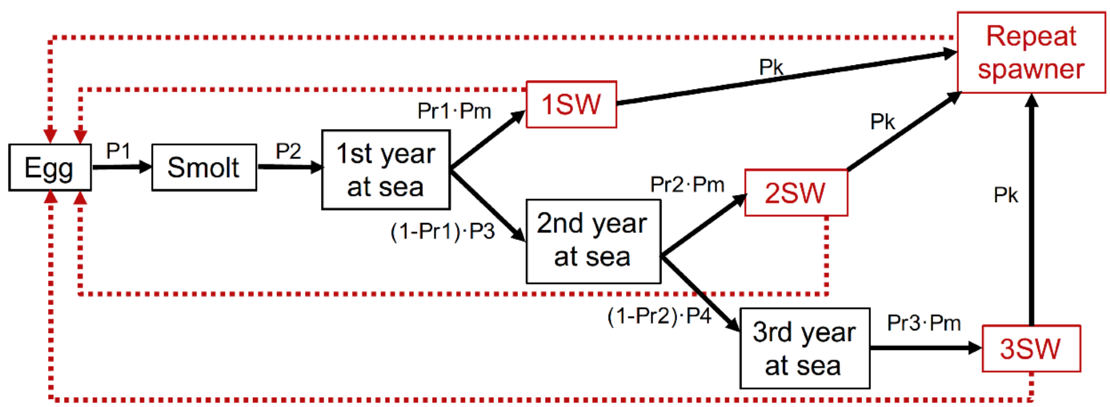

Figure 2.2: Schematic of the modelled salmon life cycle. Each life stage is represented as a box and red boxes indicate spawners. Black solid arrows represent survival between younger and older age groups and red dashed arrows represent spawners reproducing eggs.

The life-history framework described above is represented as an age- and stage-structured matrix model in (2.2). The projection matrix has the form:

$$\begin{bmatrix} 0 & 0 & Pr1 \cdot Pm \cdot F1 \cdot 0.5 & Pr2 \cdot Pm \cdot F2 \cdot 0.5 & Pr3 \cdot Pm \cdot F3 \cdot 0.5 & Prk \cdot Pm \cdot Fk \cdot 0.5 \\ P1 & 0 & 0 & 0 & 0 & 0 \\ 0 & P2 & 0 & 0 & 0 & 0 \\ 0 & 0 & (1-Pr1) \cdot P3 & 0 & 0 & 0 \\ 0 & 0 & 0 & (1-Pr2) \cdot P4 & 0 & 0 \\ 0 & 0 & Pr1 \cdot Pm \cdot Pk & Pr2 \cdot Pm \cdot Pk & Pr3 \cdot Pm \cdot Pk & 0 \end{bmatrix}$$

which determines how the population vector evolves over time.

Since individual Atlantic salmon populations in North America share common marine environmental conditions and fishing pressure in Greenland (Chaput et al., 2012), I aim to simulate their population dynamics at the scale of North America. It should be noted that the freshwater productivity (i.e., egg-to-smolt survival) is highly variable between populations both temporarily and spatially (Chaput et al. 1998), which inevitably brings uncertainty for a continental scale study. However, the freshwater within-population survival is thought to have remained fairly constant in the past two to three decades in many locations (Gibson and Claytor 2012), while the marine phase survival (i.e., survival from smolt to returning spawner) is thought to have declined since about 1990 (Chaput 2012). Therefore, I focus my analysis on the marine phase and simulate the salmon population on the continental scale.

2.3 Parameter estimates

Some of the parameter values in the matrix model are determined from the existing literature or based on assumptions, while the rest of the parameter values are determined by optimization. Which subset of parameters was chosen for optimization will be discussed later. Demographic stochasticity is taken into account by defining probability density distributions (PDF) for some of the parameters while assuming constant values for the others (Table 2.2). I will introduce how is each parameter quantified in the following paragraphs.

P1 represents the survival probability from egg to smolt. Hutchings and Jones (1998) compiled egg-to-smolt and smolt-to-grilse survival rates for 275 populations (rivers) from Europe and North America. I used the rates for populations in my study region (Maritimes, Newfoundland, Quebec and United States) only. P1 varies between 0.2-3.2% with an average of 1%. Studies show that the probability density distribution for survival of early life stages can be approximately defined as left-skewed lognormal distribution (Legault 2004), thus I defined P1 with a log-normal distribution (Figure 2.3), in which the mean equals 0.010, as previously calculated.

P2 represents the survival probability from smolt to grilse. The relevant smolt-to-grilse survival estimates from Hutchings and Jones (1998) vary between 1.3-15% with an average of 5.9%. It should be noted that this estimate already includes the return phase, which means that the smolt-to-grilse survival rate should equal the product of model parameters P2 and Pm. To compensate for this, I assumed an average of 0.6 for Pm and divided the smolt-to-grilse survival average by Pm, which yields an average of 0.098 for P2. I defined P2 with a beta distribution (similar to Lawrence et al., 2016) with a mean of 0.098 (Figure 2.3).

P3 represents the survival probability for the second year at sea. Survival estimates for the second year at sea salmon are available for two populations in Eastern Canada and vary between 10-20% and 20-60% (Chaput et al., 2003). I took the average of the two populations, which is 27.5%. This estimate again includes the return phase (i.e., P3$\times$Pm = 27.5%). I obtained P3 by dividing 27.5% by Pm and assumed that it follows a beta distribution with a mean of 0.458 (Figure 2.3).

P4 represents the survival probability for the third year at sea. Survival in fish is often assumed to increase with size (fewer predators, more prey availability as fish are growing); however, larger fish also have a higher probability to be captured by fishing assuming they are caught by trawling. Quantitative estimates of these two opposing effects are not available. Considering this, I assumed that the survival for the third year at sea (P4) equals the survival for the second year at sea (P3=0.458).

Pm represents the survival probability during spawning migration. It can be impacted by factors acting in the ocean and freshwater. Considering its large variability and lack of available observations, I made a conjecture that Pm follows a normal distribution with a mean of 0.6 (Figure 2.3).

Pk represents the survival probability from first-time spawner (1SW, 2SW and 3SW) to repeat spawner. It is set to a fixed value of 11%, which is an average value for North American salmon (Fleming and Reynolds 2004).

Pr1, Pr2, Pr3 and Prk represent the proportion of age-specific individuals to return among the 1SW, 2SW, 3SW and repeat spawners, respectively. The above parameters are known to be environmentally plastic and mediated by growth in fish (Thorpe et al., 1998). Based on a recent assessment from Massiot-Granier et al. (2014), the maturation probability of 1SW salmon varies between 40-60%. It should be noted that the Massiot-Granier et al. (2014) assessment is based on Northeast Atlantic salmon; potential regional differences are ignored here. I thus define Pr1 as a normal distribution with a mean of 0.5 (Figure 2.3) and assume a 75% probability to return as 2SW and 100% probability to return as 3SW and repeat spawners (i.e., Pr2 = 0.75, Pr3 = Prk = 1).

F1, F2, F3 and Fk represent stage-specific fecundities of 1SW, 2SW, 3SW and repeat spawners. To quantify them, I estimated the length of 1SW, 2SW and older age groups (i.e., 3SW, repeat spawner) based on data compiled by Hutchings and Jones (1998). Then I used the empirical fecundity-length relationship $F = 0.4667 \cdot L^{2.2018}$ (Fleming, 1996) to calculate the fecundities. The same length and fecundity values are used for 3SW and repeat spawners.

Table 2.2: Parameter mean values and probability density function (PDF)

Parameter	Mean	PDF	Applicable age-class	Source
Survival probability				
P1	0.010	Lognormal	Egg-to-smolt	Hutchings and Jones (1998)
P2	0.098	Beta	1st year at sea	Hutchings and Jones (1998)
P3	0.458	Beta	2nd year at sea	Chaput et al., (2003)
P4	0.458	N/A	3rd year at sea	Assumption
Pm	0.600	Normal	Migration riverward	Assumption
Pk	0.110	N/A	Repeat spawner	Fleming and Reynolds (2004)
Proportion of individuals to return for spawning				
Pr1	0.500	Normal	1SW	Massiot-Granier et al., (2014)
Pr2	0.750	N/A	2SW	Assumption
Pr3	1.000	N/A	3SW	Assumption
Prk	1.000	N/A	Repeat spawner	Assumption
Number of eggs per female				
F1	3404	N/A	1SW	Hutchings and Jones (1998) Fleming (1996)
F2	6596		2SW	
F3	8630		3SW	
Fk	8630		Repeat spawner	

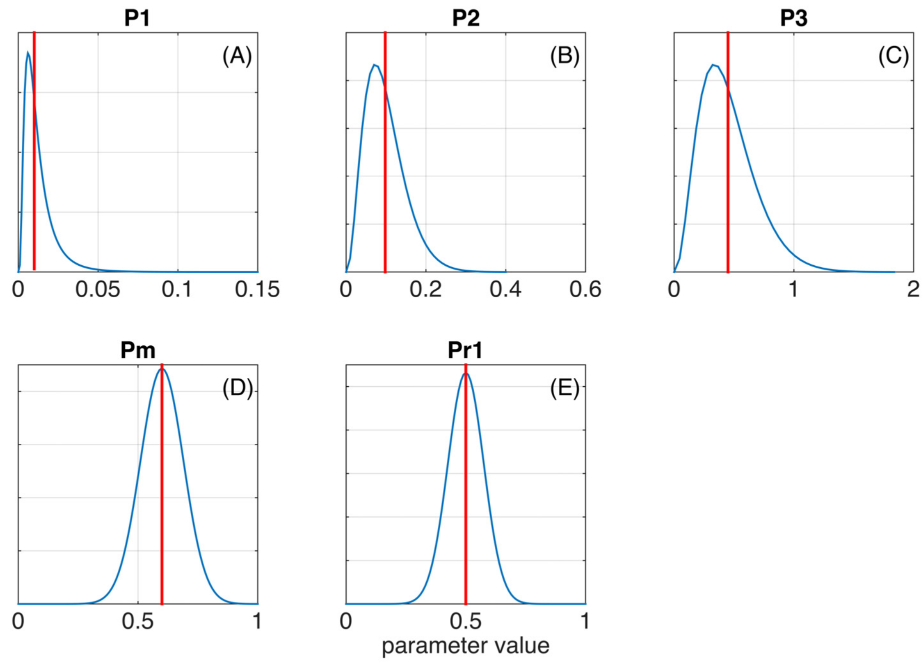

Figure 2.3: The parameter probability density distributions. Red lines indicate the mean value. (A) Lognormal distribution for egg-to-smolt survival (P1): mean = 0.01; (B) Beta distribution for survival of 1st year at sea (P2): mean = 0.098; (C) Beta distribution for survival of 2nd year at sea (P3): mean = 0.458; (D) Normal distribution for survival of migration riverward (Pm): mean = 0.6, CV of 15%. (E) Normal distribution for proportion of first year at sea salmon to return (Pr1): mean = 0.5, CV of 15%.

2.4 Data set

2.4.1 Returned 1SW and 2SW salmon

The only observation-based data available for validating and optimizing the population model are estimates of returns of 1SW and 2SW salmon to their North American spawning grounds. The returns for individual river systems and management areas were derived from a variety of methods including count observations at monitoring facilities, population estimates from mark-recapture studies, commercial catch statistics and exploitation rates (Rego et al, 1993; ICES 2015). The total returns for North America are the sum of each individual system. Uncertainty of these estimates is characterized by the 5th and 95th percentiles (Appendix A and Figure 2.4).

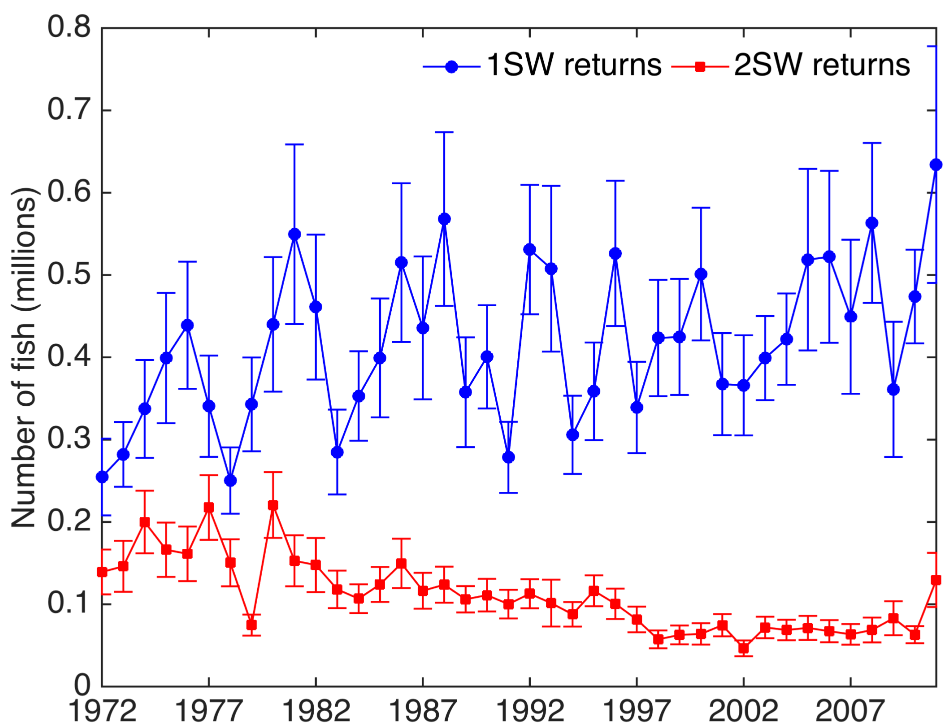

Figure 2.4: Estimated (median, 5th to 95th percentile range) returns of 1SW and 2SW salmon to their North American spawning grounds from 1972 to 2012 (ICES 2015)

2.4.2 Fishery data

Atlantic salmon may be harvested in mixed stock fisheries off West Greenland feeding grounds and near the Faroe Islands, which is referred to as the distant water fisheries (Chaput, 2012; ICES, 2015). In this thesis, I use the term 'distant water fishery' to refer to fishery near West Greenland for salmon that originated in North America only, and 'home water fishery' to refer to fishery near Canadian home waters.

For homewater fishery data, I consulted reported total nominal catch of salmon for North America (in tonnes round fresh weight) from 1960-2014, for small (1SW) and large (2SW or MSW fish) salmon in ICES (2015) (Appendix B, Table B.1, Table B.2). It is important to acknowledge that the reported landings from 1972 to 1991 likely represent considerable underestimates of the actual catches. This is because of the by-catch of salmon in the Newfoundland cod fisheries, notably the northern cod fishery along the northeast coast of Newfoundland and Labrador. I selected data covering the period of interest (1972 - 2011), and based on an average weight of 2.87kg for 1SW and 6.63kg for 2SW (ICES 2015), I calculate the average catch number for 1SW and 2SW in the homewater fishery. For simplicity, I ignored MSW and assume all large salmon belong to 2SW. For distant water fishery data, I found the reported nominal catch of North America Atlantic salmon at West Greenland from 1982 to 1992 and from 1995 to 2014 and their age compositions at sea, which are dominated by 1SW (Appendix B, Table B.3).

2.5 Optimization method

2.5.1 Evolutionary algorithm

As mentioned in section 2.3, no precise estimates exist for many of the model parameters due to challenges associated with making direct measurements in the marine environment, which is an issue that many ecosystem models encounter. To cope with this problem, model optimization techniques are frequently used in ecosystem modeling (Matear, 1995; Fennel et al, 2001; Friedrichs et al., 2006; Bagniewski et al., 2011). The basic idea is to estimate the parameter values through tuning model output to observations by manipulating the model parameters. To my knowledge, there is no study applying optimization techniques to a population matrix model. For the first time, in this thesis I aim to optimize a dynamic population model by systematically varying a set of model parameters until the misfit between the available observations and their model equivalents is minimized. The misfit is measured by a so-called cost function, similar to previous optimization studies (Wilson et al., 2013; Kuhn et al., 2015). It is defined to estimate the difference between model output and observations of 1SW and 2SW annual returns from 1972 to 2011 as follows:

$$J(p) = \frac{\sum_{j=1}^{m} \sqrt{\sum_{i=1}^{n} (S_{i,j}^{obs} - S_{i,j}^{mod}(p))^2}}{\sum_{j=1}^{m} \sum_{i=1}^{n} S_{i,j}^{obs}} \tag{2.8}$$

where $S_{i,j}^{obs}$ are observations of salmon return for year i and age class j. $S_{i,j}^{mod}(p)$ are the corresponding model outputs which depend on the vector of input parameters, p, set previously. n is the total number of years in the time series (40). m stands for the number of different age classes from which returns are quantified (2; returns of 1SW and 2SW).

The optimization is carried out through an evolutionary algorithm (Houck et al., 1995). This algorithm uses mechanisms inspired by biological evolution theories, such as selection, crossover and mutation (Figure 2.5). I start from a total of 30 initial parameter sets, which are randomly generated based on each parameter's probability density function (Figure 2.3). I then evaluate the fitness of each parameter set by calculating its cost function value. Half the parameter sets with higher cost function values are discarded and the other half (i.e., 15) with minimum cost function values will survive and act as parents of the next generation. Parent parameter sets breed new individuals through crossover (i.e., each parameter in a new offspring parameter set is randomly drawn from either one of two randomly chosen parents) and mutation (i.e., normally distributed random values with zero mean and standard deviation of 5% of the respective parameter's range is added) operations to generate offspring parameter sets. Any unrealistic parameter value (i.e., outside its predefined range) is replaced by the corresponding minimum or maximum limit. The resulting 30 new individuals (i.e., parameter sets) are then used in the next iteration. The optimization algorithm is run for 1000 generations to ensure that the cost function reaches its minimum and parameters reach an invariant state.

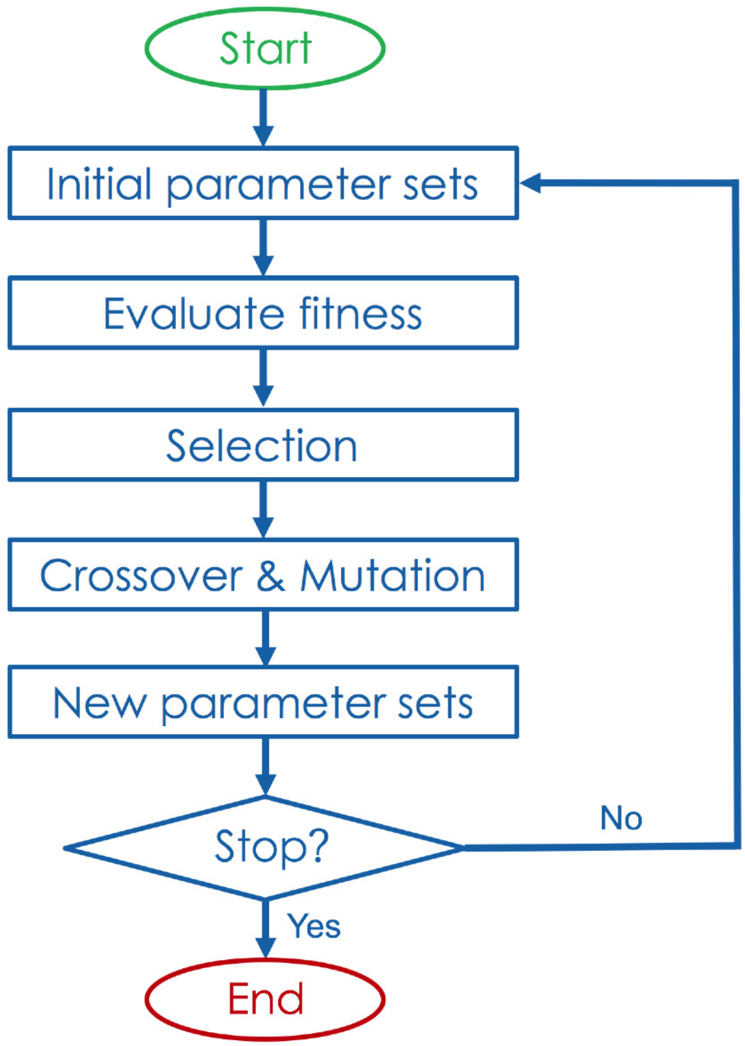

Figure 2.5: Schematic of the evolutionary algorithm

2.5.2 Hessian analysis

Previous assimilation studies have demonstrated that the optimization of ecological parameters can be challenging. For instance, Prunet et al. (1996a) showed that only some model parameters can be constrained by the observational data. Fennel et al. (2001) suggested the inadequacies in model formulation and insufficiencies of the data led to poor optimization results. Friedrichs et al. (2006) found that increased model complexity would not necessarily improve the optimization but might introduce the problem of overfitting. Initial tests in which I applied a more complex model and optimized the whole parameter set (i.e., allowed all parameters to vary at the same time) showed that these issues apply here as well. No unique optimal parameter set could be identified due to the parameter dependence problem (i.e. lack of independence between parameters). Previous studies (Thacker, 1989; Fennel et al., 2001; Friedrichs et al., 2006) showed that from calculating the Hessian matrix, one is able to investigate parameter dependencies systematically and select subsets of uncorrelated model parameters to minimize the parameter dependence problem. Another benefit of calculating the Hessian matrix is that it provides error estimates of the optimal parameters. Here we applied the same approach to determine which subset of parameters can be optimized in the Leslie matrix model.

Elements of the Hessian matrix are second-order partial derivatives of the cost function with respect to the parameters and can be estimated by perturbing the variables by a small quota and calculating the gradient of the cost function for each perturbation. The elements of the Hessian can be approximate as

$$h_{ij} = \frac{\partial F(\vec{p} + \Delta p_j)/\partial p_i - \partial F(\vec{p} - \Delta p_j)/\partial p_i}{2\Delta p_j} \tag{2.9}$$

where $\vec{p}$ represents the vector of the unknown parameters. The ratio of the Hessian's matrix largest to smallest eigenvalue is defined as the condition number of the Hessian, which measures how singular the optimization problem is (Thacker, 1989). A large condition number is undesirable for optimization because it means the function is ill conditioned with a slow convergence rate. It usually indicates that the available data are inadequate to determine all model parameters with sufficient accuracy. Additionally, by calculating eigenvalues and corresponding eigenvectors of the Hessian, one can measure the magnitude of uncertainties of the optimal parameters.

2.5.3 Twin experiment

To test whether an optimization problem is properly defined and configured, it is common to perform so-called twin experiments where 'synthetic observations' generated by the model itself are used instead of real observations. This allows one to test whether the optimal parameters, which in this case are known because they were used to generate the synthetic observations, can be recovered during optimization. Only if the optimization works well in a controlled twin experiment, can it be trusted to work with the observational data. To examine the feasibility of the optimization method for the current matrix model, I performed multiple twin experiments to address two questions: 1) is the optimization result more accurate when optimizing only a subset the parameters; and 2) how does uncertainty in the observations influence the optimization accuracy?

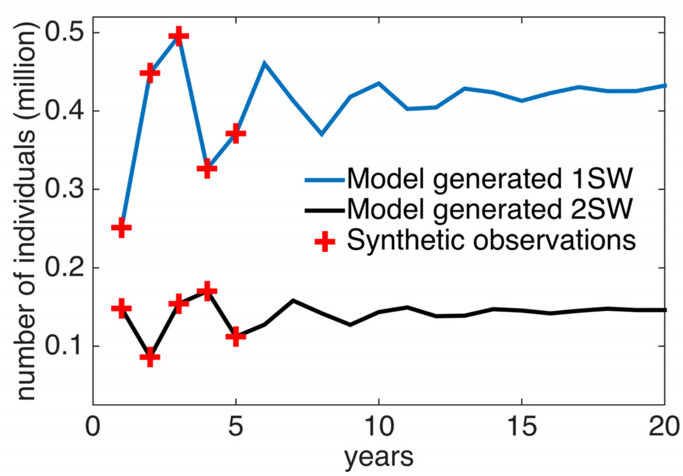

Figure 2.6: Model-generated 1SW and 2SW abundances and synthetic observations from the first 5 years used in optimization experiments A and B.

Table 2.3: Twin experiments setup, subset refers to the most sensitive 5 parameters (P1, P2, P3, Pm and Pr1. In experiments C, D and E, synthetic data are added with Gaussian errors that equal to 10%, 20% and 30% of the mean of synthetic data.

Experiments	A	B	C	D	E
Optimized parameters	All	Subset	Subset	Subset	Subset
Uncertainty added	No uncertainty	No uncertainty	10% of synthetic data	20% of synthetic data	30% of synthetic data

I set up a model case with known initial vector and constant parameter sets and ran the model for 20 years. The returned 1SW and 2SW are shown in Figure 2.6. Only the first 5 years of returned 1SW and 2SW data were sampled and used as the synthetic observations for optimization. I performed 5 different optimization experiments (Table 2.3) with perturbed initial parameters. Experiment A included all parameters in the optimization while experiment B only included a subset (P1, P2, P3, Pm and Pr1) based on the Hessian analysis. No uncertainty was added to the synthetic data in experiments A and B. In experiments A and B, the optimization was repeated 100 times and the uncertainty of the optimized parameters were quantified. Experiments C, D and E are similar to B, except that Gaussian error with variance equal to 10%, 20% and 30% of the mean value was added to the synthetic data. In experiments C, D and E, the optimization was repeated 100 times, but in each optimization, the synthetic data were randomly generated based on the Gaussian distribution, and the uncertainty of the optimized parameters was quantified as well. In this way, I allowed uncertainties from both methodology and observation to propagate into the optimized parameters.

2.6 Population model experiments

2.6.1 Sensitivity experiment

A sensitivity experiment was conducted to investigate the relative importance of the various model parameters in determining the evolution of the population. I calculated the standardized root mean square deviation (RMSD) between a baseline simulation and perturbed simulations for returned 1SW and 2SW, the perturbed simulations were conducted when only one parameter is decreased or increased by 20%.

2.6.2 Optimization over varying time segments

First, I use the 40-year time series as a whole to optimize the model, which results in one set of parameters. This case assumes that parameters are constant over 40 years, which is not necessarily realistic. Then I split the 40-year time series into 5-year segments and optimize the model for each. This generates time-dependent parameters and allows us to examine their temporal variability. The uncertainty of the observations is considered during the optimization as follows. I repeated the optimization 100 times and for each optimization, one realization of the observations (i.e., the returns of 1SW and 2SW) is randomly generated within their 5th and 95th percentile range. In this way, I allow uncertainties from the observations to propagate into the model output.

2.6.3 Optimization with fecundity parameters only

For the purpose of this study, I chose to set fecundity constant in time and focus instead on the variations of other parameters (i.e., survival probability and proportion of individuals to return). To validate this option, I performed an optimization only allowing fecundity parameters to vary, while keeping the stage-control parameters constant at their mean values. I assume a normal distribution for each fecundity with a standard deviation equal to 20% of the mean (Figure 2.7). For the initial parameter set, each fecundity value is randomly drawn based on its probability density function.

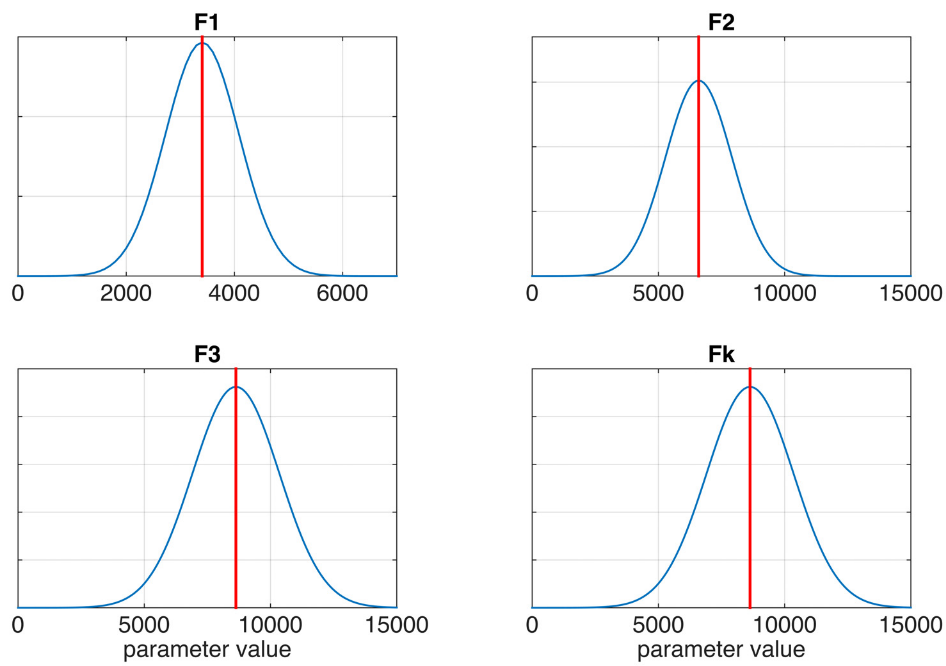

Figure 2.7: The fecundity parameters probability density distributions. Red line indicates the mean value. Fecundity parameter F1, F2, F3 and Fk follow normal distribution with mean equals 3404, 6596, 8630, 8630 respectively. The standard deviation equals 20% of the mean.

2.6.4 Incorporating fishery data

I assume that all North American salmon after their one-year migration in the ocean (1SW) reach West Greenland for feeding, and part of the 1SW age group stays near West

Greenland for another year (2nd year at sea) while the rest of the 1SW group migrates back to their natal rivers (Figure 2.8). I infer that the proportion of 1SW that stays will suffer losses from distant water fishery impacting the survival rate during the second year at sea (P3). The fraction that migrates back will suffer from homewater fishery impacting the survival rate during migration back (Pm).

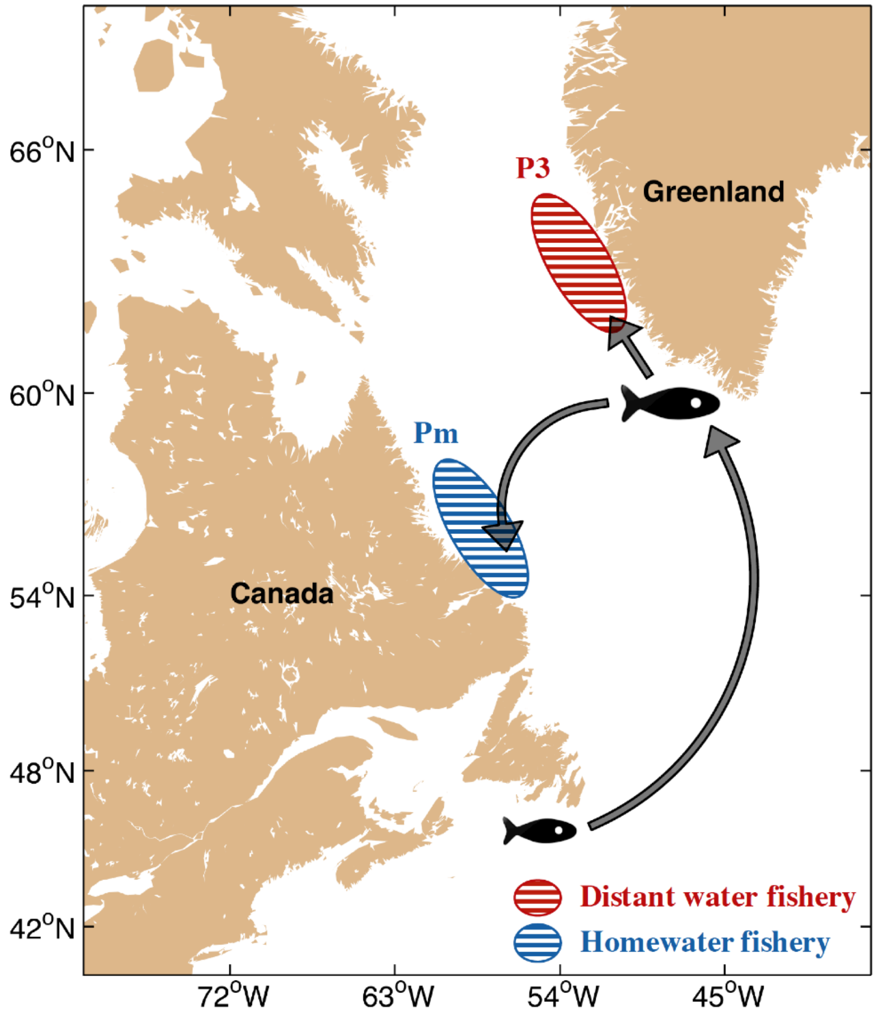

Figure 2.8: Atlantic salmon migration route and areas impacted by distant water fishery and homewater fishery. The corresponded parameters are indicated.

I aim to quantify the impact from suspension of commercial salmon fishery on parameter variations in different life stages. To do so, I combine model-simulated values with homewater and distant fishery data from 1972 to 2011. I am using the year 1972 as example to illustrate the procedure: 1) The 1SW catch in homewater in 1972 is 194000 individuals. 2) The model shows 394000 1SW individuals returning in in the same year. 3) I infer that the mortality rate inflicted by homewater fishery on returned 1SW as (1-194000/314000)$\times$100 = 49.3%. The same calculation can be applied to all years with fishery data (1972 to 2011) for both, returned 1SW and 2SW. Then I can quantify the variation of survival during migration riverward (Pm) due to the suspension of homewater fishery for 1SW and 2SW from 1972 to 2011 (Appendix B, last column of Table B.1 and Table B.2). For distant water fishery, I use model output (i.e., the non-maturing 1SW component which is going to survive through the second year at sea) and distant water fishery data to quantify the variation of the second-year survival rate (P3) influenced by distant water fishery from 1982 to 2011 (Appendix B, Table B.3).

The most important change in fisheries exploitation occurred in 1992 with the closure of the commercial salmon fishery in the waters of Newfoundland and Labrador and with the closure of the northern cod fishery, which reduced the by-catch of salmon considerably (Moore et al., 1995). Considering this, I calculated the average of survival variations (last column of Table B.1, Table B.2 and Table B.3) for all years before 1992 and for all years after 1992, and the difference between these two periods. The model can reflect the overall relative change of survival rate before and after 1992, which includes impacts from both fishery and environment. And the fishery data can inform the relative change of survival rate impacted by fishery only. Combining the two sources of information, I am able to quantify the relative roles of environmental and fishing impacts in determining parameter variations before and after 1992.

CHAPTER 3

RESULTS

3.1 Method validation

3.1.1 Hessian analysis

The Hessian matrix of the cost function (equation (2.8)) in section 2.5.1 is calculated for all parameters except fecundity. Its condition number is 8.67×10^6, indicating a nearly singular Hessian and an ill-conditioned problem formulation (Table 3.1). The parameter resolution, given by the eigenvalues and eigenvectors of the Hessian is shown in Figure 3.1. The eigenvector corresponding to the smallest eigenvalue indicates which parameters have the largest uncertainties. The smallest eigenvalue is $\lambda_1 = 3.01 \times 10^{-3}$ and the corresponding eigenvector has a significant contribution for parameter P4. Additional parameters with large contributions to the model uncertainties are Pr2 and Pk, as revealed by the second and third smallest eigenvalues (Figure 3.1). Among these parameters the ones controlling the older age class (P4 for 3rd year survival rate and Pk for repeat spawner survival rate) have the largest uncertainties. The likely explanation is that the information contained in the observations (returns of 1SW and 2SW) does not suffice to fully estimate the dynamics of these age classes.

I then repeated the analysis by subsequently removing the parameters with the largest uncertainties form the Hessian (which corresponds to excluding them from the optimization) and calculating the corresponding condition numbers and parameter uncertainties, as shown in Table 3.1. After removing the three parameters with largest uncertainty (Pk, P4 and Pr2), the condition number is reduced by two orders of magnitude to 1.06×10^5. Uncertainties of the remaining parameters (P1, P2, P3, Pm and Pr1) are much reduced, although for P3 and Pr1, the uncertainties are still large. Therefore, I chose not to optimize

Table 3.1: Condition numbers and posteriori errors for experiments E1-E4, the parameter with largest uncertainty is removed by sequence from experiment E1 to E4. All errors are scaled by the initial parameter values.

Exp.	E1	E2	E3	E4
Cond.	8.67E+06	1.76E+06	7.85E+05	1.06E+05
Post.				
P1	0.10	0.07	0.03	0.07
P2	0.35	0.39	0.38	0.37
P3	2.88	5.21	4.53	3.72
P4	28.60	17.70	N/A	N/A
Pm	4.64	1.49	1.43	1.40
Pr1	0.55	2.36	2.21	2.00
Pr2	11.80	7.48	7.20	N/A
Pk	49.20	N/A	N/A	N/A

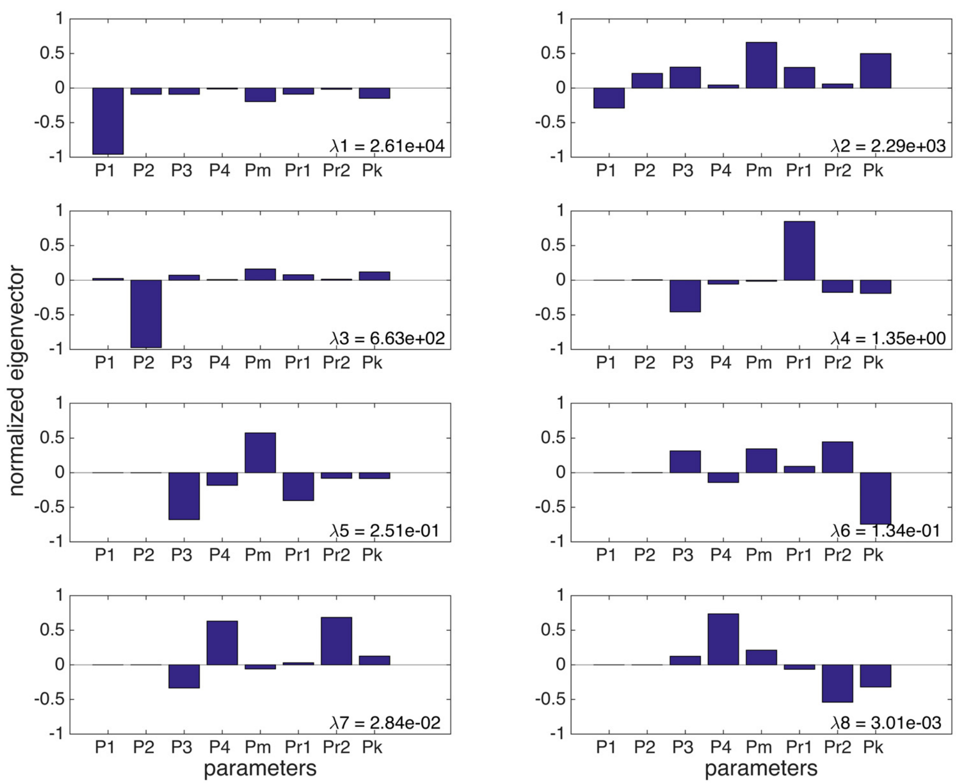

Figure 3.1: Eigenvalues and corresponding eigenvectors of the Hessian matrix of the salmon model.

Pk, P4 and Pr2. Further sensitivity experiments also show that Pk, P4 and Pr2 have the least impact on model output (Figure 3.3). It should be noted that the decision to keep part of the parameters constant is a compromise to avoid the parameter dependence problem. By performing a systematic Hessian matrix examination, I managed to reduce the number of unconstrained parameters in a systematic way while keep the feasibility of the method.

3.1.2 Twin experiment

With 5 years returned 1SW and 2SW samples and different optimization setup, I generated the optimized parameter set for P1 (egg to smolt survival rate), P2 (1st year at sea survival rate), P3 (2nd year at sea survival rate), Pm (migration back survival rate) and Pr1 (proportion to return at 1st year) and plotted them versus the real (i.e., pre-assigned) parameter values (Figure 3.2).

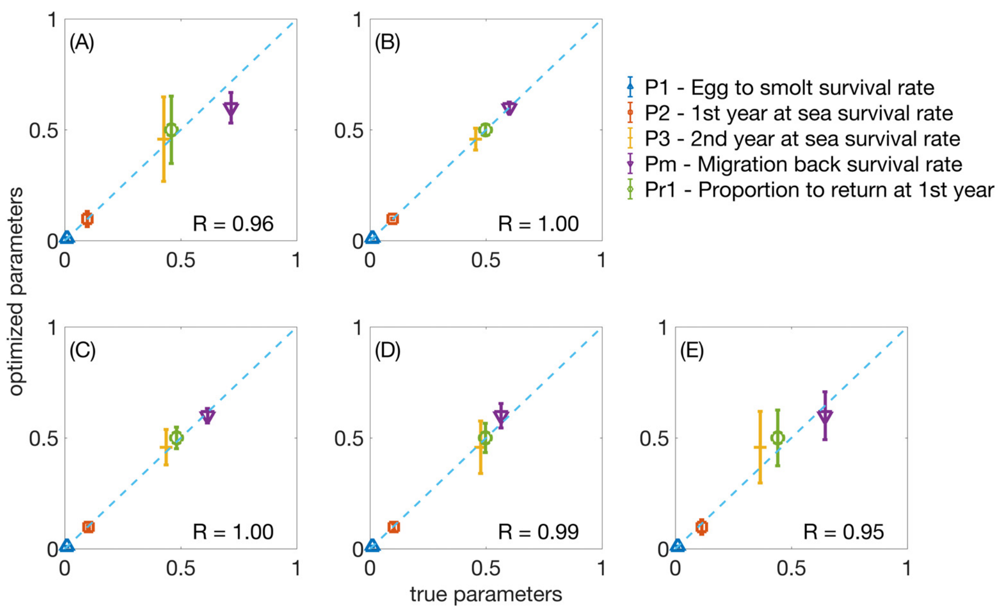

Figure 3.2: True parameters versus optimized parameters in 5 twin experiments described in Section 2.5.3. Uncertainties of the optimized parameters in experiments A and B come from the methodology (multiple optimizations) and uncertainties in experiments C, D and E come from both methodology and added Gaussian errors in the synthetic observation data.

Compared to panel A, panel B shows a much improved fit and lower uncertainty of optimized parameters, which is consistent with the Hessian analysis, corroborating that applying a subset of parameters in the optimization can effectively constrain the model. Panel C, D and E show that with increased uncertainty of the synthetic observations, correlation coefficient between optimized and true parameters decreases while the uncertainty of optimized parameters increases. The experiments illustrate that even with a subset of parameters for optimization, an appropriate uncertainty range is required for the observations to constrain the model. Panel D shows that with 20% added Gaussian error, the uncertainty of optimized parameters grows slightly, while with 30% error (Panel E) the optimization cannot capture the synthetic parameters very well, especially for P3, Pm and Pr1.

3.2 Population model experiments

3.2.1 Sensitivity experiment

The sensitivity experiment shows that the most sensitive parameters are P1, P2, P3, Pm and Pr1, the least sensitive parameters are Pk, P4 and Pr2, which is consistent with the previous Hessian matrix analysis.

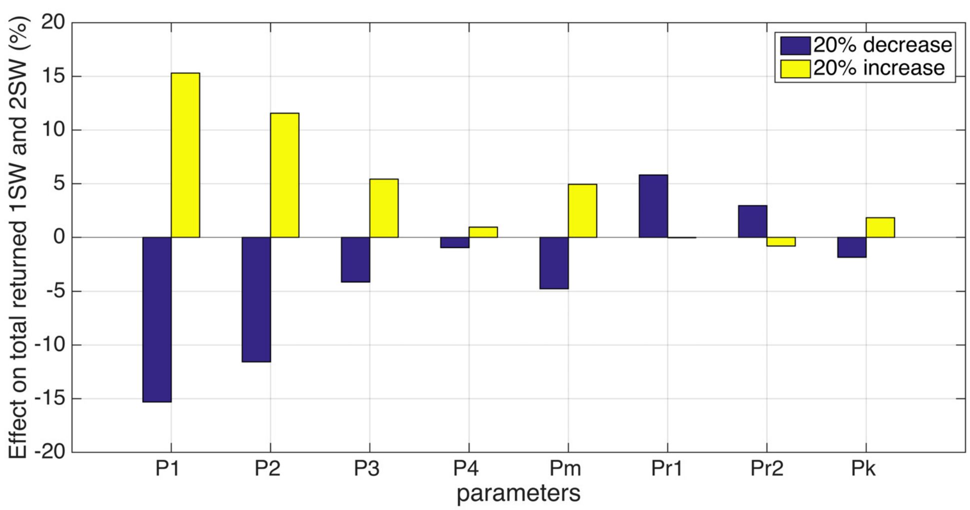

Figure 3.3: Sensitivity experiment. The blue and yellow bars stand for the variation ratio for the sum of 1SW and 2SW returns when only one parameter is decreased or increased by 20%.

3.2.2 Optimization over varying time segments

I ran the optimization over different time segments (i.e., 40-year and 5-year intervals). Model performance improves greatly with 5-year time segments compared to 40-year time segments (Figure 3.4). It is obvious that in the 40-year case, the model is not able to capture inter-annual variability and multi-year trends, while the 5-year case not only reflects annual fluctuations but also the long-term trend of slightly increasing 1SW returns and the decreasing trend in the 2SW returns. The comparison shows that introducing temporal variation of the parameters is necessary to represent the observations. The mechanisms responsible for the differing trends observed between the returns of 1SW (slightly increasing) and 2SW salmon (dramatic decline from 200 000 to 50 000) will be investigated later.

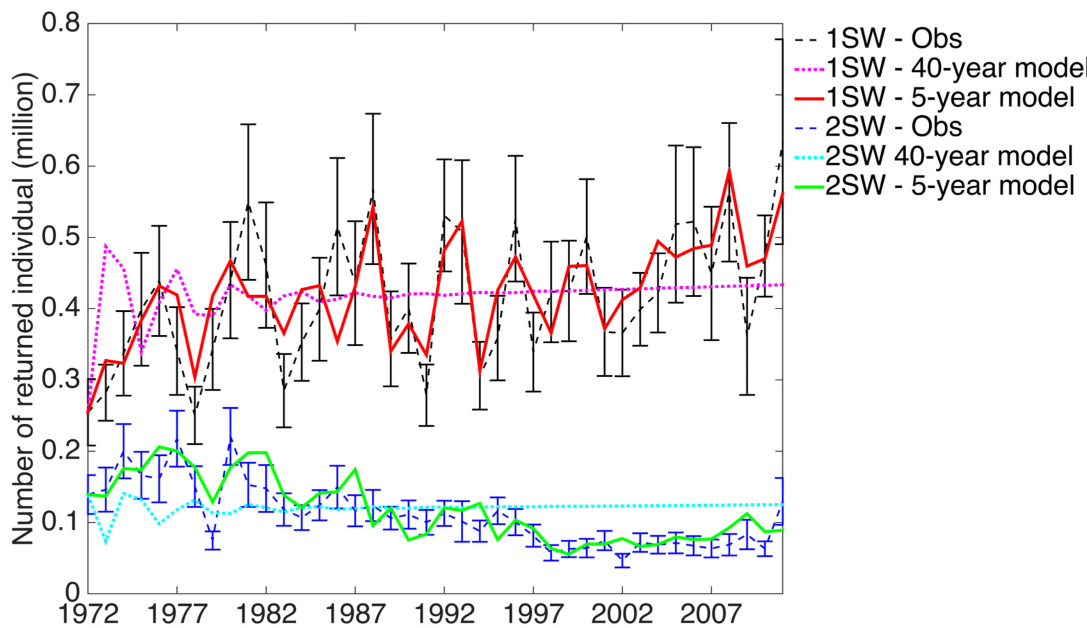

Figure 3.4: Model outputs and observations for 1SW and 2SW returns for North America from 1972 to 2011 when the optimization algorithm is applied for 40-year and 5-year time segments.

The modelling approach allows one to examine the temporal dynamics of parameters that control different life-history stages of Atlantic salmon in a general sense. Figure 3.5 shows the temporal variations for the 5 most sensitive parameters. Considering that the most important change of commercial fishery occurred in 1992, I calculate the average of all parameters from the 100 optimizations before and after 1992, and their difference, as shown in Table 3.2. The survival rate of egg-to-smolt (P1) represents the freshwater phase and the survival rate of first year at sea (P2) represents the early marine phase. Both parameters have a significant impact on the post-smolt abundance, as shown in the sensitivity experiment (Figure 3.3). But they do not contribute to the changes in proportion of 1SW and 2SW salmon returns. The survival rate of riverward migration (Pm) has impacts on all age classes simultaneously in the model, thus cannot contribute to the changes in proportion of different returned age classes neither. The remaining two parameters, the probability to return at 1st year (Pr1) and the survival rate during the second year at sea (P3), are the key parameters controlling the relative change of abundance of 1SW and 2SW returns. Further interpretation of the parameter temporal variations will be given later.

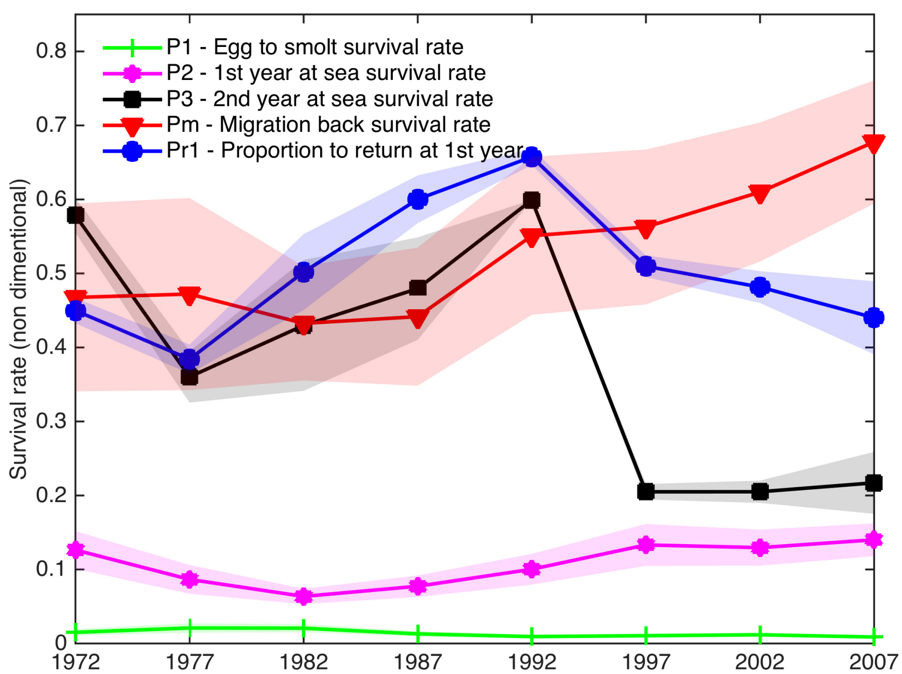

Figure 3.5: Temporal evolution of the 5 most sensitive parameters from 1972 to 2007, shaded area indicates uncertainties from both methodology and observation. The optimization was repeated for 100 times and the observations for each were drawn randomly generated between the 5th and 95th percentile range.

Table 3.2: Average and standard deviation for 5 most sensitive parameters before and after 1992 and the difference. $*$ significant at $p < 0.001$

Parameter	Before 1992	After 1992	Difference
P1	0.016±0.004	0.010±0.003	-0.006*
P2	0.091±0.018	0.134±0.025	0.043*
P3	0.489±0.043	0.209±0.022	-0.280*
Pm	0.473±0.107	0.616±0.094	0.143*
Pr1	0.519±0.026	0.477±0.028	-0.042*

To validate the idea that P3 and Pr1 are the two key parameters that control the relative change of 1SW and 2SW abundance. I performed two more sets of experiments: one experiment where P3 is set constant and the remaining 4 parameters (P1, P2, Pm and Pr1) are allowed to vary, and another experiment where P3 and Pr1 are set constant and the remaining 3 parameters (P1, P2, Pm) are allowed to vary in the optimization.

Panel b in Figure 3.6 shows that when only P3 is set constant, the model is still able to reproduce the observation well, although with a slightly increased root mean square deviation (RMSD) between model and observation (RMSD increased 10.1%, from 524059 to 577060). The parameter temporal variations (Figure 3.7) show that when P3 is set constant, Pr1 becomes the parameter exhibiting the most significant variability. It fits the expectation that an increased returning proportion of 1SW will bring higher abundance of returned 1SW and lower abundance of returned 2SW. Panel c in Figure 3.6 shows that when both P3 and Pr1 are set constant, the model has difficulty reproducing the observations, with a significantly increased RMSD (it increased 54.7%, from 524059 to 810953).

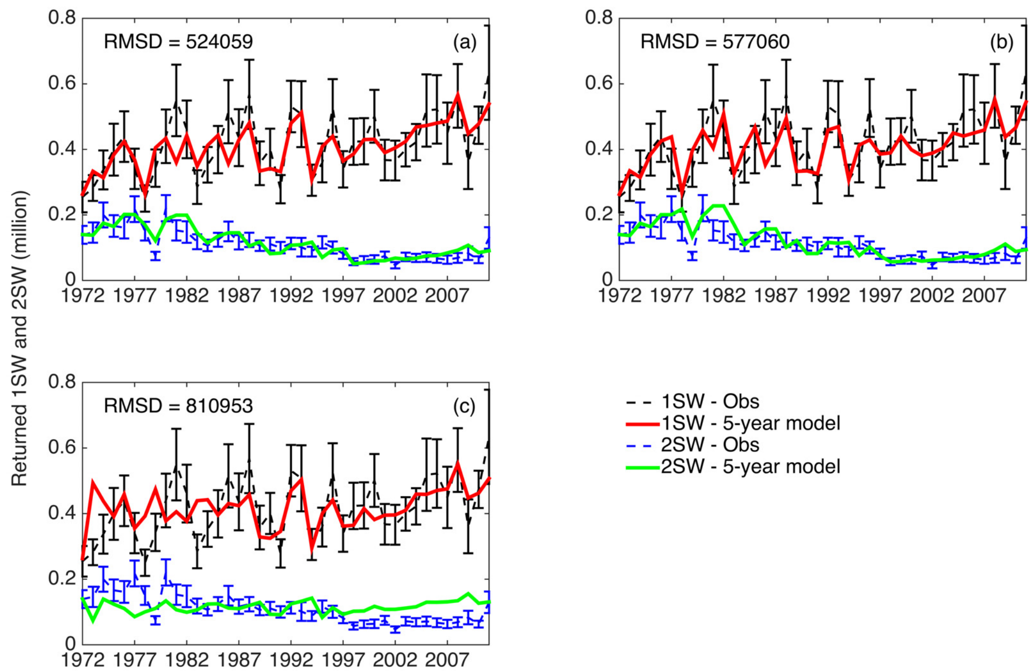

Figure 3.6: Model outputs and observations for 1SW and 2SW returns for North America from 1972 to 2011 in three optimization experiments. RMSD between model and observation is indicated. Experiment a allows 5 parameters (P1, P2, P3, Pm and Pr1) to vary. Experiment b set P3 constant and allows 4 parameters (P1, P2, Pm and Pr1) to vary. Experiment c set both P3 and Pr1 constant and allows 3 parameters (P1, P2 and Pm) to vary.

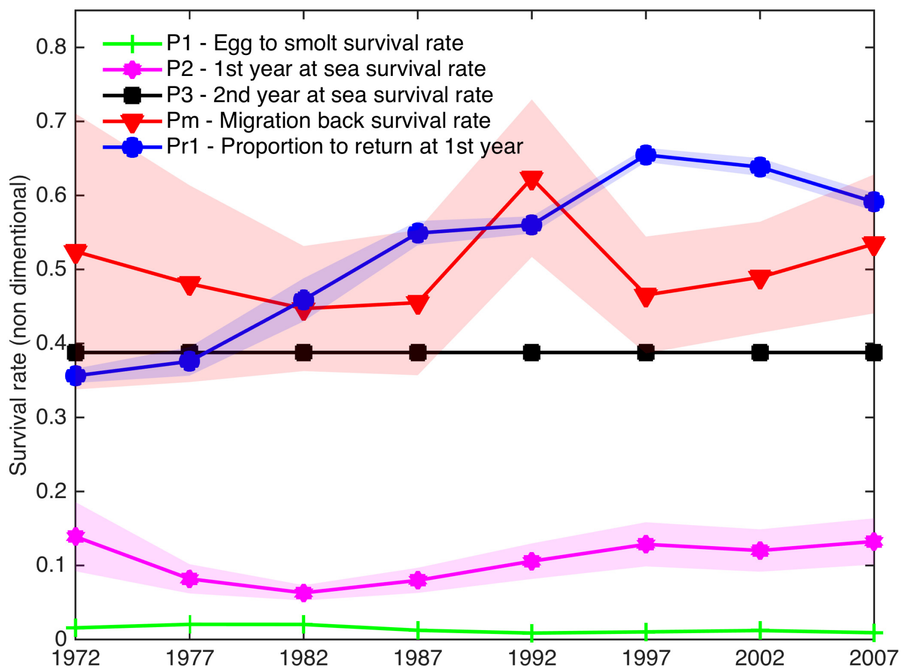

Figure 3.7: Temporal evolution of the 5 most sensitive parameters from 1972 to 2007, shaded area indicates uncertainties from observation. This optimization set P3 as constant and allows only 4 parameters (P1, P2, Pm and Pr1) to vary.

3.2.3 Optimization with fecundity parameters only

The resulting variations of the fecundity parameters appear random (Figure 3.8) and the model has difficulty reproducing the observed returns of 1SW and 2SW well when fecundity is optimized (Figure 3.9). I interpret the results of this experiment to indicate that variations in fecundity cannot produce the observed patterns of 1SW and 2SW returns. This justifies my choice to ignore the impacts from fecundity and instead focus on the stage-control parameters in this study.

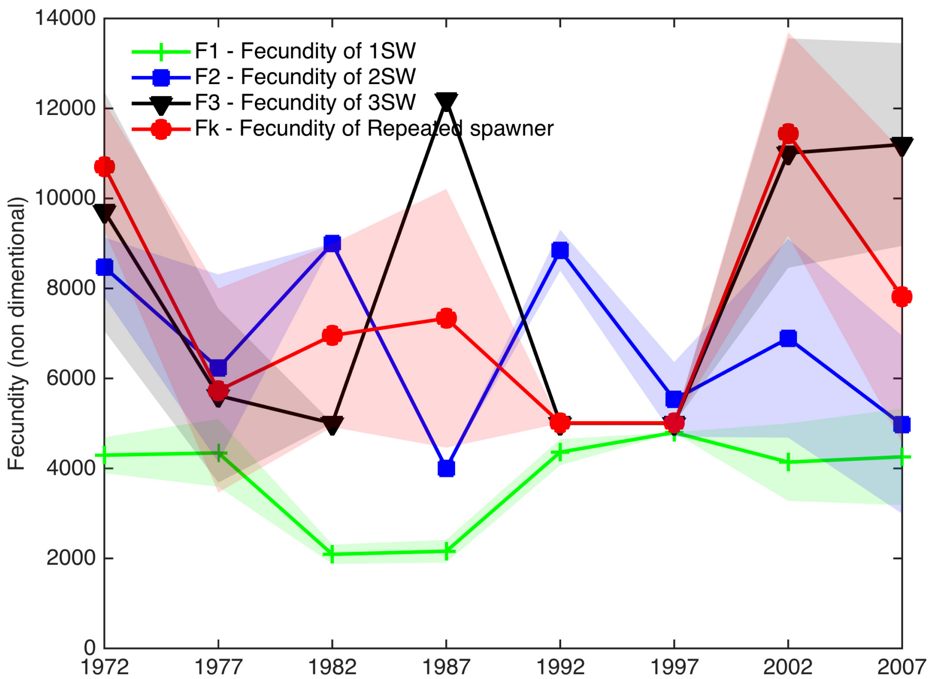

Figure 3.8: Fecundity parameters temporal variations from 1972 to 2007, shadow area indicates uncertainties.

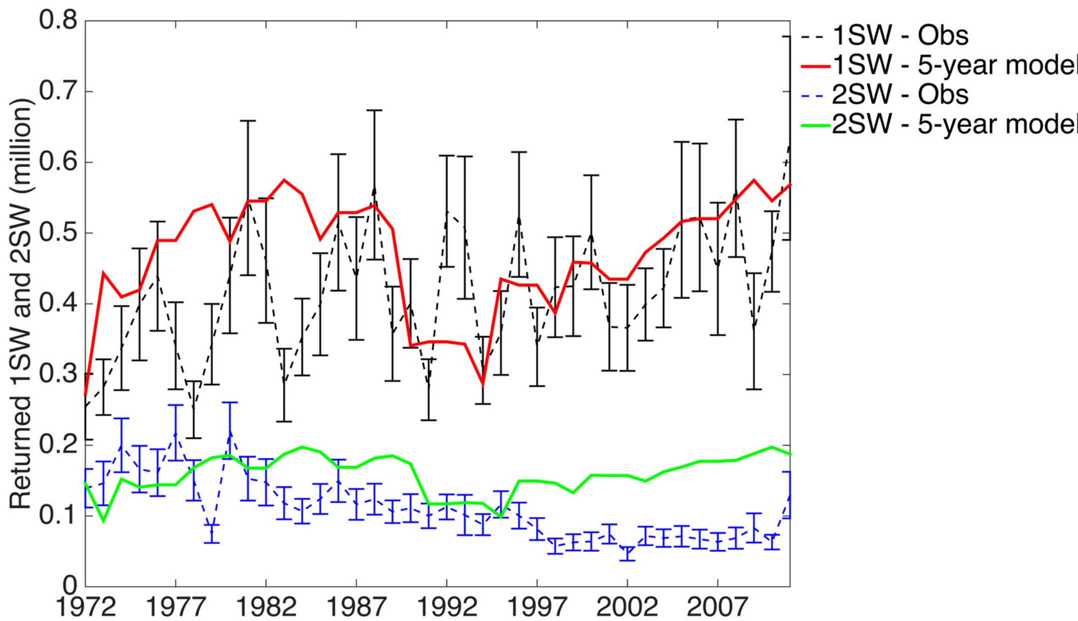

Figure 3.9: Comparison between model outputs and observations for 1SW and 2SW returns when the optimization algorithm is applied for fecundity parameters only (5-years time segment).

3.2.4 Incorporating fishery data

Using model output and fishery data, I am able to quantify the impacts from suspension of the commercial fishery on the population dynamics and, more specifically, on the parameters for survival during riverward migration (Pm) and the second year at sea (P3). Homewater suspension increases the probability of survival for 1SW and 2SW riverward migration (Pm) with increases of 25.11% and 37.70% after 1992, respectively. On average, the suspension of homewater fishery increases Pm by 31.40% after 1992. And for second year at sea survival, I find that suspension of distant water fishery increases P3 by 13% after 1992 (Table 3.3). As the overall relative change of survival rate before and after 1992 is already known (increase of 14% for Pm and decrease of 28% for P3; Table 3.2), I can infer the impact from the natural environment by subtracting the fishery impact from the total impact. This shows that the natural impact has a generally negative effect on salmon after 1992 compared to the two decades before 1992. The situation is much worse near West Greenland for the second year at sea (-41%), where the impact is twice as large compared to the natural impact in homewater (-17%). It should be noted that this assumes the population is equally sensitive to variation of Pm and P3, which is supported by results of the sensitivity experiment. The suspension of homewater fishery has a strong positive impact on survival rate during riverward migration for both 1SW and 2SW (+31% on average), strong enough to offset the negative impact from the natural environment and increase the total effect by 14% for Pm. The suspension of the distant water fishery contribution (+13%) is small compared to the harsh natural impact in West Greenland (-41%), which eventually leads to the decline of returned elder salmon. Presently, both fisheries have been reduced to historically low levels (around abundance of 50000 for homewater catch and 6000 individuals for distant water catch), but unfortunately the increased natural mortality as a response to environmental change cannot be fully offset by suspension of commercial fishing near West Greenland.

Table 3.3: Relative impact of fishing and environmental pressures on parameters Pm and P3 since 1990

	Homewater fishery suspension	Distant water fishery suspension	Natural impact	Total
Pm	+31%	N/A	-17%	+14%
P3	N/A	+13%	-41%	-28%

3.2.5 Comparison between Leslie model and ICES

As mentioned above, ICES has developed models for population assessment and forecasting, by producing an intermediate salmon abundance prior to any fisheries: The Pre-Fishery Abundance (PFA). The PFA is post-smolt abundance on January 1st of the first winter at sea prior to any fisheries. It is obtained by a hindcast analysis to resolve the unknown marine phase, aiming to provide management advice for distant water fisheries. The basic input data of the model are the same observations we used in this study (i.e., annual returns of 1SW and 2SW), which are used in the ICES model to estimate maturing and non-maturing components of PFA.

In this section, I aim to evaluate model outputs from our model approach compared to the approach used by ICES. Figure 3.10 shows the 1SW maturing, 1SW non-maturing and total cohort of 1SW from the matrix model in comparison with the corresponding PFA reported in ICES 2015. The ICES's model shows that the 1SW maturing component shows a decline since 1990, but the abundance of 1SW non-maturing cohort drops precipitously and remains at a very low abundance after about 1997. There is a significant shift in the proportion of maturing versus non-maturing 1SW (i.e., favouring an earlier maturation) after 1982-1984. However, in the Leslie model outputs, the proportion of maturing versus non-maturing 1SW is more variable. From 1972 to 1982, the proportion of non-maturing component is generally higher (i.e., Pr1$<$0.5). From 1982 to 1997, the proportion of maturing component is generally higher (i.e., Pr1 $>$ 0.5). From 1997 to 2011, the proportion of the two components is comparable (i.e., Pr1$\approx$0.5). Both models show a phase shift near 1990, which ends the decline of the total 1SW. But the ICES model shows a stable and very low abundance since 1990 and an increasing trend for the maturing component only since 2005, and an increasing trend for the non-maturing component only since 2010. Our model looks more optimistic in that the increasing trend starts near 1992, and the abundances in our model outputs are generally higher than in the ICES model. It follows that the survival rate between PFA and returns in the ICES model is generally higher compared to our model, since these two models have the same input data (i.e., 1SW and 2SW returns; Figure 2.4).

To validate the idea that the survival rate between returned salmon and PFA is set generally higher than that in the matrix model, I re-optimized the model by forcing it to generate the same output as the ICES PFA and using the same input data. In this way I

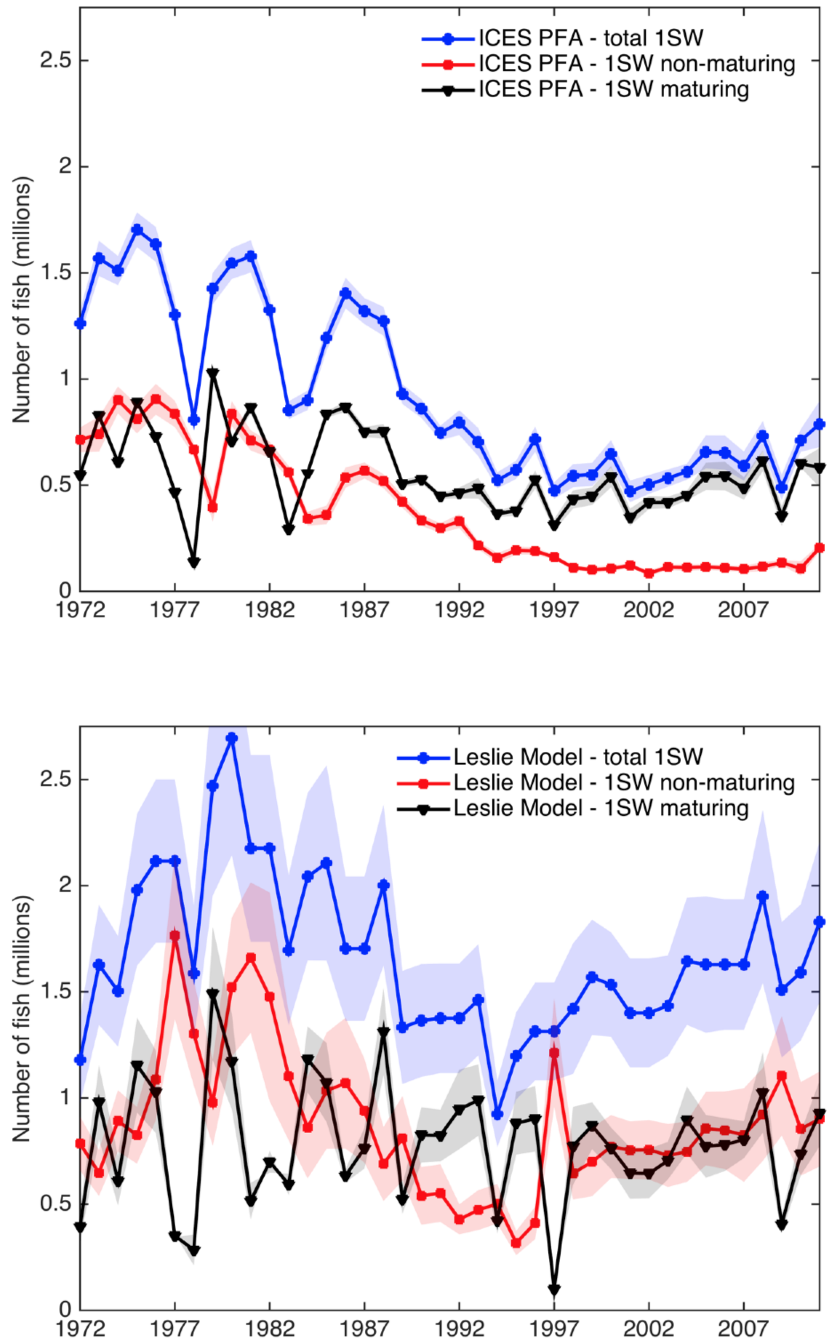

Figure 3.10: Pre-fishery abundance abundance (PFA) for 1SW maturing, 1SW non-maturing and total cohort of 1SW generated from ICES (2015) (top panel) and corresponded simulated abundance (bottom panel).

obtain the temporally varying parameters that can produce the patterns from the ICES estimates within the context of the matrix model. I then quantified temporal varying parameters (Figure 3.11) when forcing the model to produce that estimates reported by ICES (2015) within the context of the matrix model as described in section 2.2. In this analysis the second-year survival rate remains relatively constant around 0.6 except in 1987, which is higher than the second year survival rate obtained previously in the matrix model (Figure 3.5), especially after 1992. This is also roughly consistent (except for the point in 1987) with the hypothesis ICES model made that the natural mortality at sea between PFA and returns is constant over time (Rago et al., 1993; Chaput, 2012). The proportion to return at 1st year increased significantly from 1972 and remains around 0.7 since 1982. This is not surprising since under the condition that survival at sea remains constant, only an increasing proportion to return at 1st year can result in increased returning 1SW and decreased returning 2SW. This practice verified the framework's ability to use one model's output to reproduce its controlling parameters.

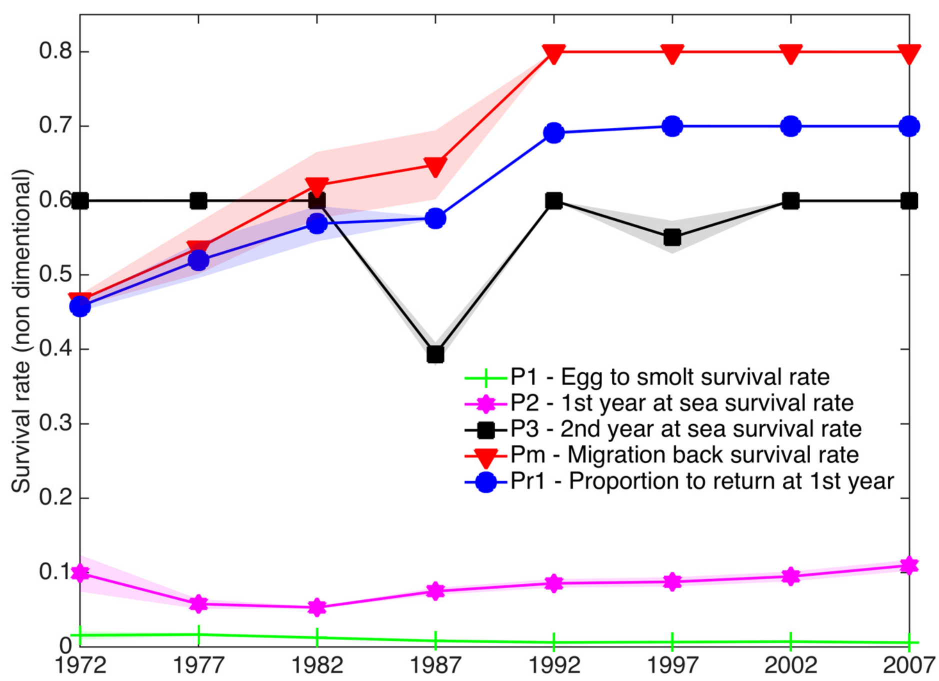

Figure 3.11: Temporal variations of the 5 most sensitive parameters from 1972 to 2007, when the model is forced to generate the same output as ICES.

CHAPTER 4

DISCUSSION

Changes in the marine ecosystem of the North Atlantic and its associated consequences for Atlantic salmon populations have been previously noted (Beaugrand and Reid, 2003; Friedland et al., 2009; Chaput 2012). Physical and biological factors can have either direct or indirect influences on salmon growth, maturity and abundance through bottom-up effects in contrast to top-down effects from fishing. In this thesis, I attempted to quantify the relative roles of environmental and fishing effects at the scale of the continental population complex. This study highlights the impacts from external environmental change on North American Atlantic salmon population dynamics and shows that the relative importance of environmental and fishing effects vary in different life stages and different regions. In the following subsections, I will discuss several issues: 1) implications from parameter temporal variations; 2) comparison between the Leslie matrix approach and the ICES model approach; 3) potential improvement of the Leslie matrix model; and 4) implications from this study for fishery management and policy making.

4.1 Parameter temporal variations

The observation-based data of returns of 1SW and 2SW salmon (Figure 2.4) shows that the abundance of returned 2SW has declined while that of returned 1SW has increased slightly. This can be explained either by an increase in the proportion maturing as 1SW or by a decrease of survival rate at sea of non-maturing fish (2SW). In this thesis, temporal variations of controlling parameters were generated using an optimization algorithm based on available observations (Figure 3.5). It shows that the probability to mature to 1SW (Pr1) fluctuated around 0.5 and had relatively small variability throughout last 40 years.

By contrast, the survival rate during the second year at sea (P3) has a significant decline between 1992 and 1997, indicating very unfavourable environmental conditions during the second year at sea after 1992. I further calculated the average value of these two parameters before 1992 and after 1997 (Table 3.2). The probability to mature to 1SW (Pr1) decreased (4.2%) from 51.9% to 47.7% (two sample t-test, $p < 0.001$) while the survival rate during the second year at sea (P3) decreased significantly (28.0%) from 48.9% to 20.9% (two sample t-test, $p < 0.001$). The changes in second year survival at sea (P3) are much greater than that of the proportion of maturing 1SW (Pr1). The results indicate that second year survival rate at sea (P3) is the key factor that contributes to the different trend of 1SW and 2SW returns.

4.2 Comparison with ICES approach

The ICES model relies on a stock-recruitment concept that considers a statistical relationship between spawning potential (eggs) and PFA (Massiot-Granier et al. 2014), which is unable to capture the dynamic link between different life-history stages. By contrast, our matrix model approach explicitly simulates Atlantic salmon's life cycle with all typical maturation types included. And I allow the parameters to vary systematically during the optimization to capture the interactions between different age groups. Our optimization approach is also more computationally efficient compared to other statistical methods (e.g., Hierarchical Bayesian Models) used for updating model state variables based on available observations.

Another weakness of the ICES model is that it assumes that natural mortality at sea between PFA and returns is constant over time (Rago et al., 1993; Chaput, 2012). This implicitly assumes that changes in the relative proportion of returns of the 1SW and 2SW age group result from changes in the proportion of maturing PFA and not in the survival rate at sea (Chaput, 2012). In this thesis, I allow multiple key parameters (including the proportion of returns of the 1SW and 2SW, survival rates at sea for 1SW and 2SW) to be optimized simultaneously and allow parameters to vary over time. The resulting temporal variations show that it is the significant decline of survival rate at sea that plays a key role in controlling the relative proportion of returns of different age groups.

Moreover, Atlantic salmon's complex life history is coarsely represented in the ICES model with lack of separation of different life stages making it difficult to incorporate available data and improve model performance. In our matrix model approach, we can easily incorporate control of varying ages of smoltification and density-dependent processes in the freshwater phase. A matrix incorporating all available life stages is flexible in testing available data, deciding where the major impact on population originates and making future projections (Browne 1988). It can also be easily applied to evaluate the performance of different management options.

4.3 Model improvement

To make the method feasible, I have to sacrifice part of the biological realism during configuration of the model. For instance, I assumed one riverward migration survival rate Pm for all age species, which may not be realistic. However, when tested with homewater fishery data, I find that the impacts from homewater suspension on 1SW and 2SW migration survival rate are of similar magnitude, which means this assumption could be validated when the fishing effect dominates the riverward migration survival.

The egg-to-smolt transition of our model could be further broken down based on varying ages of smoltification during the freshwater phase. Massiot-Granier et al., (2014) suggests that time-series of egg-to-smolt data available from a set of monitored rivers (Prevost et al., 2003; ICES 2013) could be incorporated into life-history models to provide information on density-dependent processes to improve model performance. Although the model provides overall stock-complex assessments for North American populations, it masks the regional and river-specific characteristics of Atlantic salmon populations. Atlantic salmon in different regions across their North American distribution display different life-history traits, such as different growth patterns, smoltification ages, maturation schedules, sex ratios and reproductive contributions. An area of future research would be to adjust the current model based on different life-history traits to allow applications at different population scale.

4.4 Implications for fishery management

In this thesis, I find that environmental conditions are more unfavorable near West Greenland compared to the homewater of Canada. One possible explanation is that the abundance of capelins, important food sources for salmon, has declined precipitously across the North

Atlantic subpolar gyre after 1990 (Department of Fisheries and Oceans Canada, 2011). The lack of food can negatively affect Atlantic salmon during their entire marine stage with greater cumulative effects on elder fish (Mills et al., 2013). Regional differences in predation between mid and high latitudes may also contribute. Predators distributions are shifting northward under the impact of global warming (Poloczanska et al., 2013) and may reduce salmon survival in high latitudes while improve its survival in middle latitudes.

The model provides an overall framework for hind-cast analysis of North American Atlantic salmon and could be applied to evaluate effects of fishery management options quantitatively. Based on the latest parameter mean values (2007-2011) in our model, I calculated the dominant eigenvalue λ of the matrix, which indicates increasing, stable or decreasing population trend when λ is greater than, equal to, or less than one. It turns out to be 1.0005, which means if the situation remains the same, the salmon population will be almost stable. This also warns that the suspension of commercial fishery is necessary in the short term unless the environmental conditions turn more favourable for salmon, otherwise even a small perturbation from fishing will result in a decreasing trend.

Given the recent climate-driven conditions in high latitude region appear to be unfavourable for Atlantic salmon and these conditions are expected to become even worse with climate change (Mills et al., 2013), the forecast for recovery of North American Atlantic salmon is not optimistic. While the climate and ecosystem variability are beyond the control of fisheries managers, the adaptability of Atlantic salmon populations can be reinforced at other aspects through efforts such as preventing freshwater habitat from degradation and reducing genetic pollution from aquaculture. Enhancing the population's resilience is critical for buffering climate change effects in future. Future research should focus on underlying mechanisms controlling the environmental forcings and dynamics of physical and plankton indicators. A better understanding of how environmental factors influence Atlantic salmon population can help with the design of future policies and recovery strategies.

CHAPTER 5

CONCLUSION

An integrated life-history model incorporating time-dependent parameters was developed and applied to gain insights into the population dynamics of North American Atlantic salmon over the past four decades. Temporal variations in the parameters controlling different life stages of Atlantic salmon populations were identified and show that the decline of the elder age group is subject to low survival rate during its second year at sea.

The relative impact of environmental factors and anthropogenic activity (i.e., suspension of commercial fishery) were quantified using model outputs and fishery catch data, the importance of environmental factors on salmon survival were highlighted, especially in the higher latitude region. Results suggest that the moratorium on commercial fishing is likely insufficient to induce Atlantic salmon recovery to previous abundance levels unless mitigation of environmental impacts occurs as well. However, the moratorium is crucial, at least in the short term, to maintain the relatively low yet stable abundance of Atlantic salmon.

The method presented here also provides a framework for an integrated life cycle modelling approach, especially when insufficient observations or parameter information is available. The approach helps to reconstruct the unknown phase of salmon life cycle based on exsiting observations and considers the propogation of uncertainties. This study includes populations for the whole eastern North American seaboard. Future research should apply the current model to river or region-specific data to allow inferences at different population scales.

APPENDIX A

Table A.1: Observation-based 1SW and 2SW returns (medians, 5th percentile, 95th percentile) to North American continent from ICES 2015

Year	1SW			2SW		
	median	5th	95th	median	5th	95th
1971	270442	224342	327872	110205	91037	132631
1972	254608	211958	305308	139249	113145	167640
1973	282113	243401	322103	146114	116683	178625
1974	337335	282685	401515	199942	163785	239883
1975	399124	329033	487325	166236	134039	199983
1976	439046	368264	522718	161269	130143	196385
1977	340625	284624	407716	217589	180968	259530
1978	250275	212784	293336	150391	121772	178892
1979	342820	289628	403622	74694	64502	90040
1980	440048	367341	530815	220631	182086	261999
1981	549530	450430	668710	152853	123465	185419
1982	461064	379911	556007	147704	113932	179629
1983	284955	237712	340798	118102	96578	142094
1984	353028	300683	409323	106808	91022	125892
1985	399292	330829	475316	124128	103649	146149
1986	515048	424491	617385	149694	118980	178904
1987	435808	356508	530108	116421	95683	139305

1988	568002	469593	680661	123790	102476	146223
1989	357598	295657	429009	106086	91596	123601
1990	400567	340851	466263	111076	90376	130025
1991	278520	237497	323803	100184	82813	117638
1992	530854	455663	612885	112810	95756	131121
1993	507656	411632	612910	101421	73491	130481
1994	305876	261250	356270	87802	74529	104418
1995	358733	303061	421605	116387	100111	137613
1996	526261	445515	621967	100557	83552	120399
1997	339153	290702	401688	81550	67413	98518
1998	423453	352399	493767	57384	46141	67838
1999	424839	353909	494923	62786	51034	73930
2000	501150	420368	581562	64021	51210	77279
2001	367439	305531	429500	74594	61078	88186
2002	365973	304823	426514	46467	37214	56346
2003	399050	347686	449866	71834	58846	84957
2004	422114	366154	477127	68778	55809	80682
2005	518648	407447	628003	71310	56481	85715
2006	522120	415553	624454	67322	53728	80635
2007	449339	355072	542229	63473	51387	76521
2008	563254	466117	660451	68776	54118	84267
2009	361131	279672	443893	83110	61716	103006
2010	473895	416900	530770	63105	53659	74440
2011	634139	467205	754770	129588	100936	166748
2012	484231	397806	572153	68870	53430	83489
2013	453643	324494	526853	100951	76679	129817

APPENDIX B

Table B.1: Homewater fishery data (dominated by Canada) for 1SW salmon. For each column, 1SW catch data is from ICES (2015). The abundance of 1SW catch is calculated by dividing 1SW catch data by an average weight of 2.87kg. The returned 1SW before migration is generated from model. Mortality caused by fishing for 1SW is calculated by dividing returned 1SW before migration by abundance of 1SW catch.

Year	1SW catch (tonnes)	abundance of 1SW catch	returned 1SW before migration	Mortality caused by fishing for 1SW (%)
1972	558	194425	394198	49.32
1973	783	272822	979688	27.85
1974	950	331010	610236	54.24
1975	912	317770	1155448	27.50
1976	785	273519	1028684	26.59
1977	662	230662	350877	65.74
1978	320	111498	284346	39.21
1979	582	202787	1491962	13.59
1980	917	319512	1172437	27.25
1981	818	285017	515173	55.32
1982	716	249477	699892	35.65
1983	513	178746	593463	30.12
1984	467	162718	1182288	13.76

1985	593	206620	1072771	19.26
1986	780	271777	633723	42.89
1987	833	290244	763635	38.01
1988	677	235889	1312927	17.97
1989	549	191289	522709	36.60
1990	425	148084	826116	17.93
1991	341	118815	823207	14.43
1992	199	69338	946809	7.32
1993	159	55401	989940	5.60
1994	139	48432	422419	11.47
1995	107	37282	881327	4.23
1996	138	48084	902105	5.33
1997	103	35889	100214	35.81
1998	87	30314	775290	3.91
1999	88	30662	869258	3.53
2000	95	33101	762777	4.34
2001	86	29965	646322	4.64
2002	99	34495	644346	5.35
2003	81	28223	705350	4.00
2004	94	32753	896501	3.65
2005	83	28920	772087	3.75
2006	82	28571	780762	3.66
2007	63	21951	803502	2.73
2008	100	34843	1026399	3.39
2009	74	25784	405268	6.36
2010	100	34843	736870	4.73
2011	110	38328	928386	4.13

Table B.2: Homewater fishery data (dominated by Canada) for 2SW salmon. For each column, 2SW catch data is from ICES (2015). The abundance of 2SW catch is calculated by dividing 2SW catch data by an average weight of 6.63kg. The returned 2SW before migration is generated from model. Mortality caused by fishing for 2SW is calculated by dividing returned 2SW before migration by abundance of 2SW catch.

Year	2SW catch (tonnes)	abundance of 2SW catch	returned 2SW before migration	Mortality caused by fishing for 2SW (%)
1972	1201	181146	342235	52.93
1973	1651	249020	282271	88.22
1974	1589	239668	389025	61.61
1975	1573	237255	359345	66.02
1976	1721	259578	473756	54.79
1977	1883	284012	473756	59.95
1978	1225	184766	352111	52.47
1979	705	106335	264095	40.26
1980	1763	265913	411096	64.68
1981	1619	244193	447982	54.51
1982	1082	163198	447982	36.43
1983	911	137406	338494	40.59
1984	645	97285	263511	36.92
1985	540	81448	317630	25.64
1986	779	117496	327080	35.92
1987	951	143439	327080	43.85
1988	633	95475	240083	39.77
1989	590	88989	282234	31.53
1990	486	73303	187821	39.03
1991	370	55807	192534	28.99
1992	323	48718	192534	25.30
1993	214	32278	212268	15.21

1994	216	32579	225431	14.45
1995	153	23077	142515	16.19
1996	154	23228	184941	12.56
1997	126	19005	184941	10.28
1998	70	10558	98608	10.71
1999	64	9653	106627	9.05
2000	58	8748	117806	7.43
2001	61	9201	115212	7.99
2002	49	7391	115212	6.41
2003	60	9050	111057	8.15
2004	68	10256	113821	9.01
2005	56	8446	130289	6.48
2006	55	8296	129005	6.43
2007	49	7391	129005	5.73
2008	57	8597	144748	5.94
2009	52	7843	173111	4.53
2010	53	7994	134328	5.95
2011	69	10407	141482	7.36

Table B.3: Distant water fishery data near West Greenland for salmon originated from North America. For each column, distant water fishery catch data and percentage of 1SW catch are from ICES (2015), abundance of 1SW catch is calculated as product of total fishery catch and 1SW percentage. Non-maturing 1SW is generated from the model. Mortality caused by fishing is calculated as dividing non-maturing 1SW by abundance of 1SW catch.

Year	Distant water fishery catch	Percentage of 1SW catch (%)	Abundance of 1SW catch	Non-maturing 1SW	Mortality by fishing(%)
1982	192200	N/A	N/A	1476182	N/A
1983	39500	N/A	N/A	1102297	N/A
1984	48800	N/A	N/A	859950	N/A

1985	143500	92.5	132738	1034284	12.83
1986	188300	95.1	179073	1069829	16.74
1987	171900	96.3	165540	939917	17.61
1988	125500	96.7	121359	689284	17.61
1989	65000	92.3	59995	809582	7.41
1990	62400	95.7	59717	539114	11.08
1991	111700	95.6	106785	552024	19.34
1992	46900	91.9	43101	428423	10.06
1993	N/A	N/A	N/A	472336	N/A
1994	N/A	N/A	N/A	501628	N/A
1995	21400	96.8	20715	317118	6.53
1996	22400	94.1	21078	411524	5.12
1997	18000	98.2	17676	1213415	1.46
1998	3100	96.8	3001	645922	0.46
1999	700	96.8	678	699088	0.10
2000	5100	97.4	4967	771344	0.64
2001	9400	98.2	9231	754402	1.22
2002	2300	97.3	2238	756378	0.30
2003	2600	96.7	2514	729306	0.34
2004	3900	97.0	3783	747273	0.51
2005	3500	92.4	3234	856033	0.38
2006	4000	93.0	3720	848044	0.44
2007	6100	96.5	5887	825304	0.71
2008	8000	97.4	7792	922444	0.84
2009	7000	93.4	6538	1104002	0.59
2010	10000	98.2	9820	854450	1.15
2011	6800	93.8	6378	901059	0.71

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