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Cynthia Moira Krohn
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To the Graduate Council:

I am submitting herewith a dissertation written by Cynthia Moira Krohn entitled "An Individual-based Approach to Population Dynamics with Applications to Sockeye Salmon and Iteroparous Organisms." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Mathematics.

Thomas G. Hallam, Major Professor

We have read this dissertation and recommend its acceptance:

Lou Gross, Suzanne Lenhart, Steven Bartell

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Vice Provost and
Dean of Graduate Studies

(Original signatures are on file in the Graduate Student Services Office.)

# An Individual-based Approach to Population Dynamics with Applications to Sockeye Salmon and Iteroparous Organisms

A Dissertation

Presented for the

Doctor of Philosophy Degree

The University of Tennessee, Knoxville

Cynthia Moira Krohn

August 2001

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# Abstract

Individual-based models have been used to study the population dynamics of semelparous and iteroparous organisms. The first model, developed for sockeye salmon (*Oncorhynchus nerka*), was based on the physiology of the individual and incorporated into a population model via a McKendrick-von Foerster type partial differential equation. Cycles of population abundance historically found in the Fraser River system were recreated through model simulations. Explanations for the appearance of the cycling were investigated and tested. The results showed that density- and size-dependent mortality were not necessary for cycling to appear, however their inclusion or exclusion in combination with the type of schooling could alter the character of the periodic cycling.

The use of sequential design of experiments as a method for sensitivity analysis of the model allowed for a thorough investigation of the parameter space. The approach combined standard and non-standard designs and used reverse methodology to screen for insignificant factors. The resulting sequence of designs isolated the sensitive parameters and allowed for realistic model output.

The second individual-based model was used to study iteroparous reproduction strategies and population dynamics. Two population models were formulated, a set of continuous partial differential equations of the McKendrick-von Foerster type and a set of discrete matrix equations. The asymptotic relationship between the two types of models was evaluated. It was found that a lack of convergence to the steady-state age distribution can occur in discrete event reproduction models and that convergence depends on whether the ratio between the maximum age and the length of the reproductive period is rational.

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PART I

PART II

# Introduction

This dissertation consists of three parts. The first two consider the use of individual-based models to study population dynamics while the last covers an aggregated population model.

In Part I, the life history of the semelparous sockeye salmon (*Oncorhynchus nerka*) is reviewed and the model developed based on the physiology of the individual is explained. Incorporation of the individual-based model into a population model is shown and the method of characteristics is used to reduce the partial differential equation to a system of ordinary differential equations which are solved numerically.

In order to produce realistic model output, a sensitivity analysis is conducted in Chapter 2. Methods from design of experiments, a technique used in the field of statistics, are reviewed and explained. Some of these techniques are then applied in sequential experimentation. Standard methods, such as the fractional factorial and one-factor-at-a-time, are combined with non-standard methods (saturated resolution $V$, Cotter, Plackett-Burman, and robust design) and a response surface method (central composite design) to achieve the desired result. The sensitive parameters are isolated, investigated, and subsequently used to structure a population with different ecotypes and generate values that are commensurate with a real population of salmon.

In the third chapter, simulation results demonstrate that the model produces cycles that are qualitatively similar to cycles which are known to appear in natural populations of sockeye salmon in some parts of the Fraser River system. The possible reasons for the appearance of cyclic dominance are discussed and tested using the model. The results show that mortalities associated with density-dependence and size are not responsible for the appearance of the cycles. However, density- and size-dependent mortality in combination with schooling in the freshwater environment can alter the character of the periodic cycling that occurs.

In Part II, an individual-based model is used to study iteroparous reproduction strategies and asymptotic dynamics of a population. It is assumed that reproductions are discrete events and deaths occur on a continuous time scale. In the first part of Section 3, a continuous-time model with state variables for the juvenile and adult stages is formulated and the steady-state age distribution is found. Then, a discrete-time nonlinear Leslie matrix model equivalent to the continuous-time model is derived. It is found that the population dynamics depend on the ratio between the juvenile period and the length of the periodic reproductions. If this ratio is rational, the total biomass of the population can be cyclic when the initial distribution differs from the steady-state density distribution. Additionally, the number of cohorts remains finite when they are descendants of one founder cohort. In Section 5, the discrete- and continuous-time models are compared. The case when the ratio between the juvenile period and the periodic reproductions is irrational is considered. The final section addresses the applicability of the matrix model to ecotoxicology and risk assessment.

An aggregated population model with applications to marine mesocosms is briefly discussed in Part III.

# PART I

## Sockeye Salmon Model,
## Sensitivity Analysis, and Results

# Chapter 1

# Life History and Model

## 1.1 Life History

Sockeye salmon (*Oncorhynchus nerka*) begin life as eggs deposited in the gravel of stream beds, river outlets, or shallow lakes during the Fall [29, 63, 91]. The eggs hatch within five months of deposition, depending primarily on water temperature [29, 65, 182]. The sac-fry remain in the gravel for an additional three to five weeks living on the yolk-sac [91]. Inch-long fry emerge from the spawning gravel and passively migrate to the lake by mid to late spring [29, 63, 91], at which time feeding and moving about in schools begins [91, 92, 101, 137]. The juvenile fish remain in the lake anywhere from one to four years before migrating to better feeding grounds [29, 63, 68, 91, 176, 182]. Migration from the lake is not triggered by any one factor alone, but has been speculated to include both physical and biological factors. These may include, but are not limited to, temperature, light intensity, wind intensity and direction, cloud cover, rainfall, water level, lake wave action, river discharge, age structure of the smolt population, size structure of the smolt population, and level of resource in the freshwater environment [92, 109, 110]. When the trigger for migration does occur, the smolts migrate to coastal feeding grounds in schools and then continue to the ocean [92]. The smolts mature in the ocean for one to four years, feeding heavily as there are no food limiting conditions present in this environment [57, 176, 182, 189]. Once mature, the smolts migrate back to the spawning grounds. As the salmon near the freshwater, they stop feeding and their digestive systems become nonfunctional and degenerate [35, 74, 91, 104]. Upon returning to the lake, the female digs redds (depressions in the gravel made by powerful strokes of the tail) and spawns with the male [91]. Each female spawns anywhere from three to five times, constructing a new nest in the gravel and depositing between 500 and 1100 eggs each time [35, 91]. The spawning migration and spawning activities drain 90 to 96 percent of fat and 33 to 53 percent of protein reserves [74, 104]. The spawning pair die several days after spawning has taken place.

Sockeye salmon residing in Cultus Lake, a part of the Fraser River system located in British Columbia [35], are the focus of this model. Sockeye are believed to be the principal pelagic fish of this lake [163]. The Cultus sockeye feed primarily on the following crustacean zooplankton: *Epischura nevadensis*, *Cyclops bicuspidatus*, *Daphnia pulex*, and *Bosmina obtusirostris* [61, 162]. Euphausiids are the primary food source for sockeye once they have migrated from the lake [9, 28, 176]. The majority of sockeye in Cultus Lake migrate to the ocean in April and May as year-old fish; however, a small fraction migrate during their second or third year [63, 76, 92, 162]. Nearly 90 percent of Cultus sockeye return from the sea during their fourth year of life [76].

## 1.2 Individual Model

The importance of individual-based models (IBMs) has been widely noted [23, 50, 53, 102, 103, 130, 138]. The primary reason for using an IBM to study population dynamics is that populations are made up of individuals. It is the individual which has behavioral characteristics and interacts with other members of its own population and those of other populations; it is the individual which grows, reproduces, and dies, not the population. Another reason for the IBM approach is that realistic parameter values for individuals are more accessible due to the fact that individual properties and the mechanisms by which individuals interact with the environment can be measured [103].

In order to analyze the dynamics of a realistic population, there must be some variation among the individuals which compose the population. This variation can come from any number of processes (e.g., demographic, genetic, environmental) and should depend on the study organism and the problem being addressed.

Not only is the choice to use an IBM critical, but the inclusion of lipids as one of the state variables for individual growth is also important. As stated in [82], lipid functions as the major source of energy for most fish [177]. It also regulates certain metabolic functions, is a threshold trigger and an essential component of reproduction [201], functions as a thermoinsulator, is of major importance in hydrostatic and hydrodynamic factors [177], plays an important role in overwinter starvation or survival, and assists fish in coping with environmental stressors [1]. In addition, Kooijman (1993) found that it is not possible to understand dynamics at the population level if a storage compartment is not included at the individual level. Finally, among individuals which would otherwise be considered similar, there can be substantial variation in the lipid component due to variation in the density of the resource, the quality of the resource, and other environmental stresses [84].

### 1.2.1 Model Overview

The model used here is a modification of the individual-based model for rainbow trout developed by Hallam et al. (2000) including the effects of temperature on the individual's physiological processes [131]. Hallam et al.'s model is based on the energetics of an individual female fish (see Figure 4.3).[1] Each organism is composed of two major components, lipid and structure (protein and carbohydrates), each of which consists of a labile and a nonlabile portion. The labile portions of lipid and structure are available for use in growth and reproduction; the nonlabile portions, referred to as protected, are the lipid and protein bound in somatic tissue which are not available for use, even under conditions of starvation. The mass of lipid and mass of structure are denoted by $m_L$ and $m_S$ $[g]$.[2] The mass of protected structure, $m_{PS}$ $[g]$, is assumed to be non-decreasing with age and is a constant fraction of $m_S$, i.e., $m_{PS} = \alpha m_S$; nonlabile lipid is given by

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[1] All Figures and Tables appear in the Appendices.

[2] All weights in the model are dry weights.

$\epsilon m_{PS}$ $[g]$ where $\epsilon$ is a dimensionless parameter which gives the ratio of nonlabile lipid to nonlabile structure.[3] Given these representations, the mass of labile lipid is given by $(m_L - \epsilon m_{PS})$ and the mass of labile structure by $(m_S - m_{PS})$.

The dynamics of an individual fish are represented by two ordinary differential equations which give the rates of change of $m_L$ and $m_S$. These rates are determined by the differences in the inputs and the outputs. The inputs are represented by the growth of the lipid and structure compartments whereas the outputs are the losses from these compartments. Growth of lipid and structure of a fish is obtained from feeding on a resource which also has lipid and structure components, the densities of which are denoted by $x_L$ and $x_S$ $[\frac{g}{cm^3}]$. The amount of resource that can be converted into viable energy is based on the assimilation efficiencies of the lipid and structure, represented by $A_{0L}$ and $A_{0S}$ [dimensionless] in the model. The losses consist of lipid and structure allocation for egg production and energy allocation for maintenance, apparent heat increment[4], activity, and reproduction. Maintenance, apparent heat increment, and activity losses occur on a continuous time scale; reproductive losses are discrete and occur only once for an individual given that sockeye salmon are semelparous.

The life history of a female fish is followed from the deposition and fertilization of the eggs to when the fish eventually dies. Two sets of differential equations are used to describe two different parts in the life of a fish, the yolk-sac stage and the period after

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[3] See Tables 1-6 for a list of all parameter names, their values and references.

[4] Heat increment is also known as specific dynamic action (SDA). Beamish and Trippel (1990) suggest replacing the term "heat increment" with the less-specific "apparent heat increment" due to the difficulty in experimentally separating the energy requirements for grasping, chewing, and swallowing from those of the postabsorptive processes associated with feeding.

the yolk-sac has been absorbed when external feeding commences.

The first set of equations discussed is for growth during the embryonic stage. At age 0, an egg which has the initial component weights

$$m_S(0) = m_{S_0},\, m_L(0) = m_{L_0} \tag{1.1}$$

is deposited and fertilized. The egg will hatch and survive on the nutrients of the yolk-sac until it is completely absorbed; however, since the fry are not actually feeding during this period, they decrease in size. The differential equations which represent this change in mass of lipid and structure are

$$\frac{dm_L}{dt} = \begin{cases} -B_L(m_L - \epsilon m_{PS}) & \text{for } E_D > E_A \\ -B_L(m_L - \epsilon m_{PS})\frac{E_D}{E_A} & \text{for } E_D \leq E_A \end{cases} \tag{1.2}$$

$$\frac{dm_S}{dt} = \begin{cases} -B_S(m_S - m_{PS}) & \text{for } E_D > E_A \\ -B_S(m_S - m_{PS})\frac{E_D}{E_A} & \text{for } E_D \leq E_A \end{cases} \tag{1.3}$$

where $B_L$ and $B_S$ are the compartmental rate coefficients $[\frac{1}{d}]$, $E_D$ is the total energy demand $[\frac{J}{d}]$, and $E_A$ is the available energy $[\frac{J}{d}]$. The equations for the total energy demand and the available energy will subsequently be described in detail.

The fry begin external feeding once the yolk-sac has been absorbed. The amount of time that it takes for this process to take place, $f_1(T)$ $[d]$, is assumed to be a function of temperature, $T$ $[^\circ C]$.[5]

The differential equations which describe the remainder of the organism's life are given by

$$\frac{dm_L}{dt} = \frac{A_{0L} x_L}{x} F - \begin{cases} A_L(m_L - \epsilon m_{PS}) & \text{for } E_D > E_A \\ A_L(m_L - \epsilon m_{PS}) \frac{E_D}{E_A} & \text{for } E_D \leq E_A \end{cases} \tag{1.4}$$

$$\frac{dm_S}{dt} = \frac{A_{0S} x_S}{x} F - \begin{cases} A_S(m_L - m_{PS}) & \text{for } E_D > E_A \\ A_S(m_L - m_{PS}) \frac{E_D}{E_A} & \text{for } E_D \leq E_A \end{cases} \tag{1.5}$$

where the initial conditions are given by the terminal conditions from the embryonic stage equations (1.1), (1.2), (1.3). In the above equations, $x = x_L + x_S$ $[\frac{g}{cm^3}]$, $A_L$ is the labile lipid mobilization rate $[\frac{1}{d}]$, $A_S$ is the labile structure mobilization rate $[\frac{1}{d}]$, and $F$ is the feeding rate $[\frac{g}{d}]$, which will be described momentarily. In equations (1.4) and (1.5), observe that $\frac{A_{0L} x_L}{x} F$ and $\frac{A_{0S} x_S}{x} F$ represent the gain of mass of lipid and mass of structure via consumption per unit time.

### Growth Terms

The feeding rate, $F$, can be described in terms of the characteristic time to encounter, $T_E$ $[\frac{d}{g}]$, the characteristic time for pursuit, $T_P$ $[\frac{d}{g}]$, and the characteristic time for digestion,

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[5] See Appendix II for all model functions which modify physiological processes due to temperature.

$T_D$ $[\frac{d}{g}]$, all processes which must be completed sequentially:

$$F = f_2(T)\frac{1}{T_E + T_P + T_D}. \tag{1.6}$$

The extra term, $f_2(T)$ [dimensionless], modifies the feeding rate as a function of temperature, $T$ $[^\circ C]$.

The time a non-schooling individual spends encountering one gram of food is given by $T_E = \frac{1}{a_d x}$. The encounter rate coefficient, $a_d$ $[\frac{cm^3}{d}]$, represents the volume swept per unit time by the foraging fish [72, 73] and is expressed as

$$a_d = 86400 \cdot \pi {s_d}^2 \frac{{v_p}^2 + 3{v_h}^2}{3v_h} \tag{1.7}$$

where 86400 is the conversion from seconds to days; $s_d$ $[cm]$ is the reactive distance of the fish given by $s_d = aL_p\sqrt{L_f}$; $L_f$ and $L_p$ $[cm]$ represent the lengths of the fish and prey and $a$ $[cm^{-0.5}]$ is a constant; $L_f$ is given by the allometric relationship $L_f = \sqrt[3]{\frac{m_{PS}}{\beta_f}}$ where $\beta_f$ $[\frac{g}{cm^3}]$ is a constant; $L_p$ is given by the allometric relationship $L_p = \sqrt[3]{\frac{(x_S/x)M_p}{\beta_p}}$ where $\beta_p$ $[\frac{g}{cm^3}]$ is a constant and $M_p$ $[g]$ is the mass of the prey; $v_p$ $[\frac{cm}{s}]$ is the prey velocity given by $v_p = s_p \cdot L_p$ where $s_p$ $[\frac{1}{s}]$ denotes the body lengths per second of the prey; $v_h$ $[\frac{cm}{s}]$ is the fish velocity while hunting for prey given by $v_h = s_h \cdot L_f$ where $s_h$ $[\frac{1}{s}]$ denotes body lengths per second of the fish while hunting.

If an individual is a part of a school, the encounter rate is not the same as it would be for an individual feeding alone. While in a school, it is assumed that the encounter rate, $T_E$, is modified by a schooling factor, $f_{sch}$, which is a function of the density of individuals within the school, $\rho_{sch}$:

$$f_{sch} = \frac{c_{sch}}{\rho_{sch} + c_{sch}} \tag{1.8}$$

where $c_{sch}$ is a constant. For realistic values of $\rho_{sch}$ (i.e., non-negative), the schooling factor, $f_{sch}$, only takes on values between zero and one. Note that as the density of the school approaches infinity, the value of $f_{sch}$ approaches zero.

The time an individual spends pursuing and capturing one gram of food is given by

$$T_P = \frac{s_d}{86400 \cdot M_p(v_c - v_p)} \tag{1.9}$$

where $v_c$ $[\frac{cm}{s}]$ is the velocity of the fish in pursuit and all other parameters were previously defined. $v_c$ is given by $v_c = s_c \cdot L_f$ where $s_c$ $[\frac{1}{s}]$ denotes body lengths per second of the fish while chasing a prey item.

The time an individual spends digesting one gram of food is given by

$$T_D = \frac{1}{kM_g}. \tag{1.10}$$

The gut clearance rate coefficient, $k$ $[\frac{1}{d}]$, depends on several factors. The most significant of these are fish size and temperature [31, 79]. The rate at which the mass of food in the gut empties is proportional to the mass of food in the gut, $m_g$ $[g]$ at time $t$ [59] as seen in the following equation:

$$\frac{dm_g}{dt} = -km_g. \tag{1.11}$$

Solving equation (1.11) results in $m_g = m_{g_0}e^{-kt}$ which can be rearranged to yield $k = -\frac{1}{t}ln\frac{m_g}{m_{g_0}}$. Observe that $k$ is proportional to the inverse of gut clearance time. In general, gut clearance time is proportional to (fish mass)$^{k_1}$ where $k_1$ is a nondimensional constant. Thus, $k = k_0 m_{PS}^{-k_1}$ where $k_0$ is a constant with units $[\frac{g^{k_1}}{d}]$. However, we also want to include the effect of temperature, $T$ $[°C]$, on the gut clearance rate coefficient, so $k$ is modified by a function of temperature, $f_3(T)$ [dimensionless], resulting in $k = f_3(T)k_0 m_{PS}^{-k_1}$.

Referring back to equation (1.10), $M_g$ $[g]$ is the mass capacity of the fish's gut which is calculated from the product of the volume of the fish's gut, $V_g$ $[cm^3]$, and the body density of the prey, $\rho_p$ $[\frac{g}{cm^3}]$, i.e., $M_g = \rho_p \cdot V_g$. The gut volume, $V_g$, is proportional to the mass of the fish [79] and is given by $V_g = c_g \cdot m_{PS}$ where $c_g$ $[\frac{cm^3}{g}]$ is a constant.

### Loss Terms

To calculate the loss terms for equations (1.2)-(1.5), we need formulations for the available energy, $E_A$, and the total energy demand, $E_D$. Available energy is determined by

$$E_A = 38940 \cdot B_L(m_L - \epsilon m_{PS}) + 17170 \cdot B_S(m_S - m_{PS}) \tag{1.12}$$

prior to yolk-sac absorption, and by

$$E_A = 38940 \cdot A_L(m_L - \epsilon m_{PS}) + 17170 \cdot A_S(m_S - m_{PS}) \tag{1.13}$$

once external feeding has begun. In equations (1.12) and (1.13), 38940 $[\frac{J}{g}]$ is the energetic content of one gram of lipid and 17170 $[\frac{J}{g}]$ is the energetic content of one gram of structure [74, 104].

The total energy demand, $E_D$, is the sum of the energies required for maintenance, apparent heat increment, and activity.

**Maintenance** Maintenance, also known as standard metabolism, is the minimum energy required to maintain an organism at rest [30]. The energy required for maintenance $[\frac{J}{d}]$ is given by

$$32.9m_L + 32.3m_S. \tag{1.14}$$

Brett (1976) estimated the standard metabolism of sockeye salmon to be 100 $\frac{mgO_2/kg}{hr}$ and Barton (1996) found the standard metabolism for salmonids to be between 80 and 100 $\frac{mgO_2/kg}{hr}$. Using respiratory energy equivalents of 13.69 $\frac{J}{mgO_2}$ for lipid and 13.44 $\frac{J}{mgO_2}$ for protein [30] and a standard metabolism of 100 $\frac{mgO_2/kg}{hr}$, the values of 32.9 $[\frac{J/g}{d}]$ and 32.3 $[\frac{J/g}{d}]$ in equation (1.14) were obtained.

Experimental studies have shown that increasing the temperature of the environment increases maintenance requirements of fish [5, 27, 34, 66, 67]. Therefore, equation (1.14) is multiplied by $f_4(T)$ [dimensionless] to include temperature effects.

**Apparent Heat Increment** Apparent heat increment is defined as the metabolic heat loss from the digestion and transformation of food into energy [30]. Beamish and Trippel (1990) reported that fish fed natural diets have an apparent heat increment value between 3 and 41%, while fish fed formulated diets have values between 11 and 29%. They also found that apparent heat increment increases with meal size and body weight, as well as with temperature, but declines with body weight when food intake is fixed. The value of apparent heat increment is generally lower for lipids than for protein because lipids do not have to be deaminated to serve as an energy source [132]. Brett and Groves (1979) attributed 12-16% of ingested food energy to apparent heat increment. Following the study for rainbow trout reported by Beamish and Trippel (1990), the value for apparent heat increment is given as a function of temperature, $f_5(T)$ [dimensionless].

**Activity** Cruising, the cost of pursuit and capture of food, and migration are all activities which incur an energy loss. The energy utilized by a swimming fish $[\frac{J}{d}]$ is calculated using a formulation by Gerritsen (1984):

$$\frac{0.002376 S v^{2.5}}{L_f^{0.5} q} \tag{1.15}$$

where 0.002376 has units of $\frac{Js^{2.5}}{cm^4 d}$; $S$ $[cm^2]$ is wetted surface area given by $\beta_2 {L_f}^2$ where $\beta_2$ is a non-dimensional proportionality constant for wetted surface area; $v$ $[\frac{cm}{s}]$ is the swimming velocity (part of the time spent on cruising and part on chasing food) which is the product of fish length, $L_f$, and the number of body lengths per second spent on either cruising or pursuing; and $q$ [dimensionless] is swimming efficiency.

Remember from equation (1.6) that time spent feeding is divided between encounter, pursuit, and digestion. Of these, the "active" times are the times spent finding and capturing prey items. Therefore, $T_E F = \frac{T_E}{T_E+T_P+T_D}$ [dimensionless] is the time in days per daily ration encountered and $T_P F = \frac{T_P}{T_E+T_P+T_D}$ [dimensionless] is the time in days per daily ration captured. Hence, the total active time per day is $(T_E+T_P)F$. Incorporating these formulations into equation (1.15), the new equation for the energy expense due to swimming is:

$$\frac{0.002376\beta_2 {L_f}^4({s_h}^{2.5}T_E F + {s_c}^{2.5}T_P F)}{q} \tag{1.16}$$

which is in terms of parameters that have all been defined previously.

While the model presented here is not spatially-explicit, migration is accounted for by a loss of energy. The formula that represents this energy loss is:

$$\psi_x \cdot \zeta_x(m_L + m_S) \tag{1.17}$$

where $\psi_x$ $[\frac{J/g}{km}]$ is the migration cost per unit distance (if $x = 1$, the migration is from the lake to the coastal feeding grounds; if $x = 2$, the migration is from the ocean to the river entrance; if $x = 3$, the migration is from the river entrance to the lake), and $\zeta_x$ $[\frac{km}{d}]$ is the rate of travel when migrating. The value used for the distance from the lake to the coastal feeding grounds and river mouth is 110 $km$ [61, 76]; the distance from the ocean to the river entrance used is 3000 $km$ [78].

### Reproduction and Mortality

Reproduction is a loss term, however, it is not explicitly stated in equations (1.4) and (1.5). Reproduction is not assessed on a continuous basis as are the terms associated with maintenance, apparent heat increment, and activity. For sockeye salmon, reproduction occurs only once, and after reproduction occurs, the salmon dies. In the model, an individual can die if one of two conditions is met. One, the mass of structure drops below the mass of protected structure associated with starvation (this level is given by $\alpha_1 m_{PS}$ where $\alpha_1$ is a constant), which occurs either due to losses associated with reproduction or due to a shortage of resource. Or two, the individual reaches the prescribed maximum age, $a_{max}$.

In order for reproduction to occur in the model, three conditions must be met. The first is that the individual must have survived the first five life history stages (see the discussion following on Migration) and be in the final stage in the lake. Next, the time of year must be within the time window for reproduction, September 1 to December 31 [65, 166]. And, finally, the temperature must be between 3 and $20°C$ [78, 166, 175].

The losses associated with reproduction include allocation of lipid and structural mass to egg formation and the energy necessary to complete this mass transfer. While it is clear that these events occur on a continuous time scale, there is little specific information on the time scales of these processes. Since the time scales are short relative to the population time scales, they are treated as discrete events.

Lipid and structural mass available for reproduction constrain the number of eggs that an individual can produce. Although variation in egg size is most likely controlled by a number of factors, the assumption is made that it is controlled solely by lipid. The amount of structure per egg is assumed to be constant. The governing factors for allocation of lipid to eggs are assumed to be total lipid ($m_L$) and a counteractive coupling with total structure. If $E_S$ $[eggs]$ is the maximum number of eggs that can be produced from the available structure, then the lipid allocated to each egg is given by the hyperbolic function (in $m_L$)

$$\frac{(e_{max} - e_{min})m_L}{A_1 E_S + m_L} + e_{min} \tag{1.18}$$

where $e_{max}$ and $e_{min}$ $[\frac{g}{egg}]$ are the maximum and minimum amounts of lipid contained per egg. $A_1$ $[\frac{g}{egg}]$ is a constant which in some sense determines the relative importance the female places on lipid in the eggs, and hence, the size of the eggs at birth. While this function gives values in the interval $[e_{min}, e_{max})$, the maximum lipid contained in an egg, $e_{max}$, is only attained asymptotically as lipid becomes large. Observe that the maximum number of eggs constrained by available structure, $E_S$, regulates the egg lipid: for fixed lipid, $m_L$, the amount of lipid per egg decreases as $E_S$ increases. The maximum number of eggs per available lipid is determined by dividing the total lipid, $m_L$, by the amount of lipid per egg.

A formulation to set $E_S$, the maximum number of eggs per available structure, is also needed. Weatherley (1972), using data from [2], found that the number of eggs laid by trout in the Horokiwi stream can be determined, at least in a restricted range, as a linear function of body length. Carlander (1969) also reported this type of representation. Using this as a basis for our formulation, the maximum number of eggs produced per available structure, $E_S$, by a female of length $L_f$ is given by

$$\min\left\{\max[0,\sigma(L_f-\eta)],\frac{m_S}{e_s}\right\}. \tag{1.19}$$

The term $\sigma(L_f-\eta)$ gives the number of eggs per clutch as a linear function of fish length. The slope, $\sigma$ $[\frac{eggs}{cm}]$, is generally a function of resource availability, but is a constant here. $\eta$ $[cm]$ is a constant which determines the smallest length at which reproduction can occur, resulting in a positive number of eggs when subtracted from the fish length. The second expression is the structural material available for reproduction, where $e_s$ $[\frac{g}{egg}]$ is the amount of structure per egg. Weatherley (1972) argues, for trout, that the size at reproduction is a governing factor for reproduction. This is taken into consideration by composing a size constraint for reproduction and requiring that there be sufficient lipid and structure to form the eggs.

Given the number of eggs that could possibly be produced based on available lipid and the number of eggs that could possibly be produced based on available structure, the number of eggs that are actually produced is the minimum of these two constraints. The egg composition, assumed to be a fixed amount of structural material and a variable amount of lipid, varies according to the lipid reserves of the adult female.

It is assumed that a fraction of the eggs produced do not survive due to the physical environment. The fraction of eggs that survive given as a function of temperature, $T$ $[^\circ C]$, is given by $f_6(T)$ [dimensionless].

The energy required to support the mass transfer of lipid and structure to eggs is modeled by $A_2 L_e + A_3 S_e$. $L_e$ and $S_e$ $[g]$ are the total lipid and structure in the eggs; $A_2$ and $A_3$ $[\frac{J}{g}]$ are rate constants for the energy to mobilize lipid and structure for eggs. This formulation is similar to the one for allocation to maintenance.

### Migration

In the model, there are six life history stages:

Stage 1: In the lake, as an egg or fry

Stage 2: Smolt migrating from the lake to the coastal feeding grounds/ocean

Stage 3: Juvenile in the ocean

Stage 4: Juvenile migrating from the ocean to the river entrance

Stage 5: Juvenile migrating from the river entrance to the lake

Stage 6: In the lake, as an adult.

The stage in which an individual is determines whether or not feeding and schooling occur, which temperature function is used, which resource is seen, and which particular losses take place (see Table 7). External feeding occurs in stages 1 (post yolk-sac), 3, and 4; schooling occurs in stages 1 (post yolk-sac) and 2.

There are two temperature functions used in the model, one to simulate the temperature in the lake and one for the temperature in the ocean. The basic formulation for the temperature function, $T$ $[^\circ C]$, is

$$T(t_J) = \begin{cases} \frac{T_{high}-T_{low}}{2}\sin\left(\frac{\pi}{t_{peak}}t_J + \frac{3\pi}{2}\right) + \frac{T_{low}+T_{high}}{2} & \text{for } 0 \le t_J \le t_{peak} \\ \frac{T_{high}-T_{low}}{2}\sin\left(\frac{\pi}{365-t_{peak}}(t_J - t_{peak}) + \frac{\pi}{2}\right) + \frac{T_{low}+T_{high}}{2} & \text{for } t_{peak} \le t_J \le 365 \end{cases} \tag{1.20}$$

where $t_J$ is the Julian day of the year, $T_{low}$ $[^\circ C]$ is the low temperature which occurs in the lake or ocean, and $T_{high}$ $[^\circ C]$ is the high temperature which occurs in the lake or ocean on Julian day $t_{peak}$. The values used for the ocean environment are from [26] and [28]; the values used for the lake are from these as well as [63].

The resource utilized by the salmon in the lake environment is different from that seen in the ocean. In the lake, the prey item is parameterized to simulate the zooplankton *Cyclops bicuspidatus*; *Cyclops* appear to be the sockeye's primary food item and are consumed in every season [61, 76, 162]. Euphausiids are the primary food source for sockeye once they have migrated from the lake [9, 28, 176]. In the model, the ocean resource is assumed to be *Thysanoessa spinifera* [176].

In the model, the cue to migrate from one environment to the next is governed by three factors. The first criteria is that the individual must have at least a specified threshold mass. For migration from the lake, an individual must weight at least 6 (wet) or 1.55 (dry) grams [28, 35, 100, 108]; for the spawning migration, an individual must weight at least 1400 (wet) or 434 (dry) grams [28]. The second and third criteria that must be met are a combination of temperature and season. For the smolt migration to occur, it must be the first six months of the year and the temperature must be between

4 and 17.5°$C$ [35, 63, 78, 90, 92]; this corresponds to the spring time. Due to a lack of temperature information for the spawning migration, the final criteria for the migration from the ocean is only the correct time of year, which is mid-June to mid-September [28].

### Schooling

While it has been explained (in the section which discusses growth terms and in Appendix III) how schooling modifies the model equations through the encounter rate and size-dependent mortality, the actual implementation of schooling in the code requires further explanation.

The creation of schools in the freshwater environment is based upon the value of $idiv$, the maximum possible number of schools, and the minimum and maximum lengths of all fish in the freshwater environment at each time step. Once the minimum and maximum lengths are known, this interval is subdivided into smaller intervals using the value of $idiv$. Every fish in the freshwater environment then fits into one of these subintervals. Naturally, it is possible for some subintervals to be empty, which is why $idiv$ is the maximum *possible* number of schools, and not the actual number of schools. The purpose of implementing schooling in this manner is to group individuals of similar length together, as this is how it has been suggested that fish school in their natural environment [3, 45]. Given that the size interval of all the fish in the freshwater environment is recalculated at each time step, changes in the total number of schools, the number of individuals within each school, and the association of an ecotype with a specific school are all possible. This reorganization of schools at each time step is supported by [154] where it is noted that schools frequently undergo repeated organization.

## 1.3 Population Model

To study the dynamics of the population, the individual growth model is incorporated into a system of hyperbolic partial differential equations of extended McKendrick-von Foerster type:

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} + \frac{\partial(\rho \cdot g_L)}{\partial m_L} + \frac{\partial(\rho \cdot g_S)}{\partial m_S} = -\mu(\rho) \cdot \rho \tag{1.21}$$

where the population density function, $\rho = \rho(t, a, m_L, m_S)$, is given in numbers per age ($a$), per mass of lipid ($m_L$), per mass of structure ($m_S$), per volume of environment. The growth rates of the lipid and structure compartments, represented by $g_L$ and $g_S$ $[\frac{g}{d}]$ respectively, are calculated from equations (1.2) and (1.3) or equations (1.4) and (1.5), depending on the life history stage of the fish. The mortality rate is given by $\mu$ $[\frac{1}{d}]$ and the birth process is specified by a boundary condition which can be represented in the following manner:

$$\rho(t, 0, m_{L_0}, m_{S_0}) =$$

$$\int_0^\infty \int_{m_{S_0}}^\infty \int_{m_{L_0}}^\infty \beta(t, a, m_{L_0}, m_{S_0}, m_L, m_S)\rho(t, a, m_L, m_S)\ dm_L\ dm_S\ da. \tag{1.22}$$

The birth function, $\beta$, represents the number of eggs with lipid content $m_{L_0}$ and structure content $m_{S_0}$ born to an individual of age $a$ with lipid content $m_L$ and structure content $m_S$ at time $t$.

The mortality rate is stated explicitly in equation (1.21) and consists of the sum of a few different types of mortality: age-dependent, size-dependent, density-dependent, and young-of-the-year (when appropriate). See Appendix III for details on each type of mortality.

The method of characteristics is used to reduce equation (1.21) to a system of ordinary differential equations:

$$\begin{aligned} \frac{da}{d\lambda} &= 1 \\ \frac{dt}{d\lambda} &= 1 \\ \frac{dm_L}{d\lambda} &= g_L \\ \frac{dm_S}{d\lambda} &= g_S \\ \frac{d\rho}{d\lambda} &= -\left(\mu + \frac{dg_L}{dm_L} + \frac{dg_S}{dm_S}\right)\rho \end{aligned} \tag{1.23}$$

which are valid along the characteristic curves, where $\lambda$ is the characteristic parameter. This system of equations is solved numerically in the simulation approach used here.

While any number of individual ecotypes can be used to represent the population, here the initial population is composed of 243 different types of individuals. Each ecotype is described by its own partial differential equation in the form of equation (1.21), resulting initially in a population model consisting of 243 equations. The actual parameters used to induce variability in the individuals, and hence the population, were determined by the results of the sensitivity analysis and will be discussed in Section 2.2.

## 1.4 Other Models

As stated in the article by Hallam et al. (2000), other authors have implemented models which investigate energetics and growth in fish populations. Many of these articles are based on the work by Kitchell et al. [112, 113]. The dynamics at the population level are typically derived by multiplying single fish dynamics by estimates of the population size and cohort mortality rates [87]. Some populations which have been explored are the bluegill [112], yellow perch and walleye [113], largemouth bass [161], lake trout [181], sockeye salmon [13], and kokanee [183]. Hewett and Johnson (1992) created a generalized bioenergetics model and provided physiological parameters for twenty species. Some authors have expanded these population models to include temporal and spatially explicit relationships [17, 20, 157, 158]. For further applications of these types of models, see [87, 97, 98]. See also [187] for a more detailed overview of some of the models mentioned here.

Age-structured models for fish have also been developed [48, 51, 52]. In [49], the authors used an individual-based approach to analyze the dynamics of smallmouth bass populations.

As was mentioned previously, the model presented here is a modification of a rainbow trout model [82], which was originally based on a model for *Daphnia* [85]. Other models which have been developed also for *Daphnia* and which use a similar philosophy to the one presented here can be found in [83, 118, 138]. The details of the models are, however, dependent on the study organism, and therefore, will be different from the sockeye salmon individual and population models described here.

# Chapter 2

# Sensitivity Analysis

Sensitivity analysis investigates the effect that small changes in input parameters have on the model outputs of interest. By determining which parameters have a significant effect on the model output and which parameters have comparatively little influence, we are essentially determining which parameters control the model. While there are many methods available to perform sensitivity analyses [86, 105, 173, 195], the technique used here, known as design of experiments (DOE), is borrowed from the field of statistics. Some advantages of using DOE are that interactions between parameters and the effect of these interactions on the outputs of interest can be accounted for; the number of simulations performed can be kept to a minimum while maximizing the information that can be extracted from the results; polynomial-type behavior can be investigated; and, sequential experimentation can be used. Using DOE also makes it possible to produce a highly simplified approximation model to the computer model, which is analogous to regression analysis.

## 2.1 Methods from Design of Experiments

Different methods within the DOE setting have been used to perform sensitivity analyses of simulation models. In this section, a description of various designs and examples of where each has previously been used as a tool for sensitivity analysis of computer models can be found.

Before presenting examples of the use of DOE as a sensitivity analysis tool, some background information on the actual methods from DOE is given. There are a wide variety of texts which explain DOE, some give a broad presentation [139], while others are specific to a particular method. See [114] for an overview of some statistical methods applied specifically to simulation models.

In the following subsections, the input parameters, or factors, will be represented by capital letters. If there is interaction between any parameters, meaning that the effect of one parameter on the output is dependent upon the level of another parameter, it will be represented by combining the factors involved in the interaction. For example, if a model has three input parameters, they will be represented by A, B, and C. If there is interaction between, say, parameters B and C, this will be represented by BC. The effect that a change in the level of an individual factor has on the output of interest is typically called a *main effect*.

Finally, keep in mind that my outlook on the use of DOE as a tool for sensitivity analysis is on deterministic models, i.e., there is no random error component in the models being considered. Therefore, we are not concerned with measures of statistical significance, only the magnitude of the estimated effects and interaction effects of the parameters on the model output. Furthermore, the order in which the simulations are completed is not important. Note that the computer models from the literature given as examples in the following sections are not necessarily deterministic.

### 2.1.1 Standard Methods

There are several types of designs which are commonly used in DOE. The reasons for their predominant use range from ease of design and analysis to their balanced and orthogonal properties. These will be referred to as standard designs and include full and fractional factorials. One-factor-at-a-time designs are also discussed here.

#### One-factor-at-a-time Designs

The one-factor-at-a-time method can take on many forms, but is just as it sounds. Most typically, each simulation is run with all factors held at their base level except for one. If each factor is being varied by one level, the number of simulations performed will be equal to the number of inputs to the model plus one extra simulation where all the parameters are left at their base values. This approach does not allow for the estimation of interaction among parameters.

This method was used in [185] as an example of a crude sensitivity analysis approach of a model which investigated the net present value of a gas transmission system on the

Indonesian island of Java. The author notes that the one-factor-at-a-time method is the most popular one in applied problems and cites some examples. One-factor-at-a-time sensitivity analysis, referred to as differential sensitivity analysis in Lomas and Eppel's (1992) paper, was also used to study three simulation programs which aided in the design of passive solar buildings [129]. The authors compared this method to two other non-DOE methods.

Note that the original model on which this dissertation is based was for a model of *Daphnia* [85] which was subsequently modified to model rainbow trout [82]. The sensitivity analysis used in [85] was a one-factor-at-a-time method.

### Full Factorial Designs

A full factorial design takes every possible combination of every parameter with every other parameter, at each level under consideration for each parameter. Full factorials can be run at any number of levels ($\geq 2$) for each factor, however, the most common use of the full factorial is with factors that vary across two levels. Thus, the two-level full factorial is typically referred to as a full factorial. From this two-level full factorial, it is possible to estimate both the main effects of the parameters and *all* the interaction effects on the model output. It is not possible to estimate quadratic effects, i.e., terms of the form $A^2$, $B^2$, etc. However, quadratic effects for individual parameters can be estimated by utilizing more than two levels for a factor.

As an example, if we have three parameters, each with two levels to investigate, a full factorial design will result in running $2^3 = 8$ experiments. (In the computer model setting, each "experiment" is actually a single simulation of the model.) For this two-level example, if we use "+" to represent running a parameter at its high level and "−" for its low level, then the treatment combinations which would result in the eight simulations would be:

$$\begin{array}{ccc} A & B & C \\ - & - & - \\ + & - & - \\ - & + & - \\ + & + & - \\ - & - & + \\ + & - & + \\ - & + & + \\ + & + & +. \end{array} \tag{2.1}$$

From these simulations, it is possible to understand the effect that A, B, and C each have on the model output. Additionally, the interaction effects AB, AC, BC, and ABC explain how the effects of A, B, and C change as the levels of other factors change. This is just a small example of the full factorial design. Keep in mind that this design can quickly result in a huge number of simulations, depending on how many parameters are involved and at how many levels. If we had 30 parameters, each at two different levels of interest, we would have to run $2^{30} = 1,073,741,824$ simulations. If we assume that each run takes one second, it would take just over 34 years to complete all the simulations and the amount of data created would probably take just as long to analyze!

It is not possible to estimate quadratic effects using a full factorial design, however if the model under consideration is deterministic, we can add one more simulation (at the "center") which will allow us to estimate the sum of the quadratic effects. From this, we can at least determine if quadratic effects are significant. If necessary, this design can be sequentially augmented to form a central composite design (discussed in Section 2.1.3) to estimate all quadratic terms.

Full factorial designs have been used to study the sensitivity of model outputs to the input parameters in a number of models, but primarily when the number of parameters was small. The following examples are for three inputs at two different levels. The full factorial design was used to find the effect of model inputs on production cost for a model of a system for ethanol production from woody biomass [77], on the output of a coal transportation model [115], and on a model which illustrated the impact of plating defects on the reliability of vias and Plated Through Holes [46]. The full factorial design was also used for sensitivity analysis in a model for invasive plant spread with five parameters [99] and in a model which was used to study the relationship between landscape patterns and the spread of mistletoes [124]. Other examples may be found in [89].

### Fractional Factorial Designs

Fractional factorial designs are subsets of full factorial designs and are the most common designs used. An often performed role of the fractional factorial design is parameter screening. These designs can be as small as $2^{k-p}$ $(> k)$, where $k$ is the number of input parameters and $p$ is an integer which will be further explained in the next paragraph. In statistics, screening experiments are used prior to more detailed analyses to identify the dominant factors among a large number of factors. When there are a large number of parameters, it is typically assumed that the output is determined primarily by just a few main effects and low-order interactions which implies that the higher-order interactions are assumed to be negligible. This is known as the *sparsity of effects principle*.

Two-level fractional factorial designs are referred to either as $2^{k-p}$ fractional factorial designs or as a $\frac{1}{2^p}$ fraction of the $2^k$ design. (See [18] for a full explanation of this design.) $k$ is the number of parameters and $p$ is the number of dependent parameters. The number of simulations performed is $n = 2^{k-p}$ and the given Roman numerals explain the confounding properties of the design, where confounding and aliasing mean that effects are inseparable from each other during analysis. The number of simulations is reduced from the full factorial case by aliasing $p$ individual parameters with higher-order interactions. This aliasing is explained by the resolution of the design.

Resolution $III$, $IV$, and $V$ designs are the most common and were the ones primarily found in the literature. In general, a resolution $III$ design has main effects aliased with two-factor and higher-order interactions. A resolution $IV$ design has main effects aliased with three-factor and higher-order interactions, and two-factor interactions aliased with other two-factor and higher-order interactions. A resolution $V$ design has main effects aliased with four-factor and higher-order interactions, and two-factor interactions aliased with three-factor and higher-order interactions. The design used will depend on the number of parameters in the model as well as the lowest order interactions which can be assumed to be negligible. For example, a ten parameter model with all interactions assumed negligible can utilize a $2_{III}^{10-6}$ design ($n = 16$) which allows for estimation of all main effects. However, if it is only reasonable to assume three-factor and higher-order interactions are negligible, but we want to estimate both the main effects and two-factor interactions, a $2_{V}^{10-3}$ ($n = 128$) is required. In practice, with some prior knowledge as to which interactions are important, a $2_{IV}^{10-5}$ design ($n = 32$) with a well planned alias structure could possibly be used.

For clarity, an example of a resolution *III* design is given here. If we have a model which has six parameters, each at two levels of interest, then we can generate a $2_{III}^{6-3}$ design by first generating a full factorial in $6 - 3 = 3$ parameters (see (2.1)) and then aliasing the remaining three parameters with interactions involving the first three parameters. The treatment combinations would be:

$$\begin{array}{cccccc} A & B & C & D & E & F \\ - & - & - & + & + & + \\ + & - & - & - & - & + \\ - & + & - & - & + & - \\ + & + & - & + & - & - \\ - & - & + & + & - & - \\ + & - & + & - & + & - \\ - & + & + & - & - & + \\ + & + & + & + & + & + \end{array} \tag{2.2}$$

if we assumed that D=AB, E=AC, and F=BC.

A resolution $III$ design can be increased to resolution $IV$ by using the *fold over principle.* Fold over is accomplished in this situation by executing the simulations that would result if we reversed the sign of every treatment combination used to create the resolution $III$ design. This results in breaking the links between the main effects and the two-factor interactions with which they are aliased, allowing the main effects to be estimated clear of any other two-factor interactions. Fold over techniques may be used to increase all odd resolution designs to the next highest even resolution design; see [139] for more details.

Folding over the resolution $III$ design given in (2.2) would result in the following sequential design:

$$\begin{array}{cccccc} A & B & C & D & E & F \\ + & + & + & - & - & - \\ - & + & + & + & + & - \\ + & - & + & + & - & + \\ - & - & + & - & + & + \\ + & + & - & - & + & + \\ - & + & - & + & - & + \\ + & - & - & + & + & - \\ - & - & - & - & - & -. \end{array} \tag{2.3}$$

If we look, for example, at D which is supposed to be equal to AB from the aliasing structure chosen previously, we see that this no longer holds true (D=-AB); therefore, when this fold over is combined with the original $2^{6-3}_{III}$ design, D is no longer aliased with AB. We now have a resolution $IV$ design as a result of only 16 simulations.

Fractional factorial designs are considered *orthogonal* because effects are either perfectly correlated (via the alias structure) or perfectly uncorrelated with other effects. Conversely, a *non-orthogonal* design can have some partially correlated effects, however, they typically require fewer simulations.

Fractional factorial designs have been used as a tool for sensitivity analysis of a number of models across a wide variety of fields, however, the authors in [96] noted that full and fractional factorial designs have not been used to a great extent in environmental modeling. They proposed using these designs and gave examples from the fields of numerical global climate modeling, air pollution management decision support systems, and water quality modeling. Although not found to any great extent in the ecological modeling literature, note that fractional factorial designs were brought to our attention as a method for performing sensitivity analysis in [169]. The author compared different sensitivity analysis methods and applied the fractional factorial design method to a model of phytoplankton growth.

Kleijnen (1997) discussed designs of resolution $III$, $IV$, and $V$ in his paper and cited some examples. A $2_{IV}^{24-16}$ design was used to analyze the sensitivity of a model which simulated the air flow and pollutant transport in a three-story building [69]. The authors compared this method to the Monte-Carlo method and discussed a hybrid of the two. Fractional factorial designs were also used as a sensitivity analysis method in a study of an energy-system model for multi-family buildings [80], for a model of a wastewater treatment system [184], for a model of environmental radionuclide movement, and for a model of salt dissolution in bedded salt formations [105].

A $2_{III}^{5-3}$ sensitivity analysis was conducted on a model of a residential desuperheater [125]. This article is actually an example of the misuse of DOE. While there is nothing wrong with using this as a screening design to estimate the main effects, the conclusions drawn for the designed experiment reported were incorrect. The authors found that some two- and three-factor interactions were significant; this cannot be determined from the design that was presented because these higher-order interactions were aliased with the main effects. A correct analysis of the results and an explanation of the misuse is given in [120] (see Appendix IV).

### 2.1.2 Non-standard Methods

Non-standard designs are typically non-orthogonal, and, therefore are useful when random error is minimal. In the case of deterministic models, where there is no random error, non-standard designs become a viable option as a tool for sensitivity analysis.

The designs discussed in this section, Group Screening, Plackett-Burman, Cotter, Saturated Resolution $V$, Taguchi Designs, and Robust Parameter Design, are among the countless number of non-standard designs available. Another set of non-standard designs, not discussed in detail here, are the optimal designs (e.g., D-Optimal, A-Optimal, G-Optimal), which are computer generated using an algorithm with criteria specific to the type of optimality.

#### Group Screening Designs

Group screening designs were first introduced by Watson (1961). In this type of design, factors are assigned to groups and sequential experiments are required. Although group screening designs can be performed in different ways, the basic methodology is as follows: multiple factors are grouped together to form a smaller number of "new factors" on which experiments are performed. This design is in essence a resolution $II$ design, where follow-up experimentation can focus on factors involved in groups identified as significant in previous experiments. It is possible to incorporate a group screening procedure into the other types of designs described in this chapter by treating a group of factors as an individual factor and running the design with the new groups as the factors.

An overview of group screening is given in [40] and [179]. The use of group screening in combination with factorial designs and central composite designs was discussed and then applied to a simulation of a flight simulator in [40]. The Plackett-Burman design and group screening were used in [155]. In an endnote, Kleijnen (1987) cited a variety of examples of group screening designs.

**Sequential Bifurcation** A modification of Jacoby and Harrison's (1962) group screening method, sequential bifurcation, was introduced in [15] and applied to a model for the assessment of the greenhouse effect [16]. In [15], the author compared the modified sequential bifurcation method to two-stage group screening [135, 136, 196], multi-stage group screening [127, 148], and briefly to a group screening method by Morris (1987). The sequential bifurcation method was compared to Morris' factorial sampling method [141] and used in the sensitivity analysis of a building thermal model in [47].

**Iterated Fractional Factorial Design** A new group screening method which is a variation on fractional factorial design is the iterated fractional factorial design (IFFD) [4]. IFFD can be used to estimate main effects and two-factor interactions of the important parameters and can also be expanded to estimate quadratic effects. It has been demonstrated that the success of this method depends strongly on the number of influential parameters there are to find and weakly on the total number of parameters; the best results were found when the model output was dominated by a small number of highly influential parameters. IFFD has difficulty dealing with higher than quadratic order effects [172] and tends to give incorrect results in situations where there are many equally important parameters [171]. The IFFD method has been used to find the influential parameters in a probabilistic assessment model of environmental impacts from the disposal of used nuclear fuel [4].

### Plackett-Burman Designs

Plackett-Burman designs are actually a subset of the two-level fractional factorial designs. They are used for analyzing up to $n-1$ parameters in $n$ simulations where $n$ is a multiple of four. However, if $n$ is a power of two, the designs are the same as that of the two-level fractional factorial case. Plackett-Burman designs which do not reduce to two-level fractional factorial designs are generated in an unusual manner and have complex aliasing structures where factors are partially aliased with a number of interactions (see [139] and [151] for details). Interpretation of these designs can be complicated and the probability of both false positives and false negatives with respect to the significant factors is much higher than with standard designs.

The Plackett-Burman design with fold over was used to find the sensitivity of a model which estimated economic risk [185, 186]. In [186], the authors discussed fractional factorial design, the Plackett-Burman design and compared these methods to Monte-Carlo analysis. The one-factor-at-a-time approach was compared to the Plackett-Burman design in a case-study of a model which investigated the net present value of a gas transmission system on the Indonesian island of Java in [185]. A sensitivity analysis using the Plackett-Burman design was also used in a model for the Ground water Loading Effects of Agricultural Management Systems (GLEAMS) [44], in a model which simulated the transport of chemicals in soil [93], and in combination with a group screening technique in a building thermal model [155].

### Cotter Design

The Cotter design was introduced in [43] and was originally called the systematic fractional replicate design. The purpose of this design is only to identify the parameters which are highly influential or are involved in interaction effects which are highly influential, not to model their effects. These parameters can then be further explored with other designs. The primary advantage of the Cotter design is that no prior assumptions about interactions are made and there are no alias chains to untangle, as with other designs. The Cotter design is a modification of the one-factor-at-a-time approach. For a model with $k$ parameters which vary across two levels, $2k+2$ simulations are needed. The first simulation is run with all parameters at their low level. The following $k$ runs maintain the form of the first simulation with the exception that one factor in turn is chosen to be run at its high level. The next $k$ simulations are run with every factor at its high level except for one which is, in turn, at its low level. The last simulation is run with all factors at their high level. The last $k+1$ runs are in effect the same as folding over the first $k+1$ runs. The Cotter design estimates the sums of all odd order effects involving each factor and all even order effects involving each factor. This means that for each factor, there is an estimate which is composed of the sum of the main effect and all odd-order interactions in which it is involved. The second estimate for each factor is the sum of the estimates of all even-order interactions in which the factor is involved. It is cautioned, however, that false negatives with respect to factor significance are possible due to cancelling of effects.

In the current literature, I have been unable to find any simulation models which implement the Cotter design as a method for sensitivity analysis. It is mentioned here because it is one of the methods I use in the sensitivity analysis of the individual model in Section 2.2.

### Saturated Resolution $V$ Designs

Saturated designs generate only enough information to estimate effects, with no information left to estimate error. Using saturated designs to analyze the sensitivity of a deterministic model, where random error should be zero, does not pose a problem. Saturated resolution $V$ designs were introduced in [160]. The estimation of the main effects and two-factor interactions is possible in a design of resolution $V$.

As with the Cotter design, I did not find the saturated resolution $V$ design used anywhere in the literature as a tool for sensitivity analysis. I include it here because it is used in the sensitivity analysis of Section 2.2.

### Taguchi Designs

Taguchi methods are used to overcome the limitations that come with running a full or fractional factorial on a model which has a large number of parameters. Taguchi designs are a set of carefully chosen orthogonal arrays taken from the full factorial design. In setting up a Taguchi design, one must select the most suitable orthogonal array and assign the parameters to the appropriate columns based on prior knowledge of the system. The orthogonal arrays for two-level parameters are denoted by $L_4$, $L_8$, $L_{16}$, $L_{32}$, … where the subscript indicates the number of simulations to be performed for up to four parameters (noninclusive) for the $L_4$ design, between four and seven parameters for the $L_8$ design, etc. For tables of orthogonal arrays and more details on setting up a Taguchi design, see [170].

Taguchi designs work well when interactions among factors are minimal, however, if an interaction is thought to be important, it can be included by assigning the interaction to its own column. The Taguchi design makes the assumption that the relationship between the parameter values and the output values is linear; when this assumption is violated, the Taguchi method may produce meaningless results [39]. Note that this assumption does not imply that the Taguchi method assumes that the actual model is linear. See [39] for a discussion of other benefits and limitations of this type of design.

Clemson et al. (1995) compared Latin hypercube sampling and the Taguchi design and applied the latter to a model of a conventional activated biosolids wastewater treatment plan. Raju and Pillai (1999) used an $L_{32}$ Taguchi design for their sensitivity analysis of a multicriterion decision making tool for the performance evaluation of an irrigation project in India. A mixed-level Taguchi design was used in [55], where the authors investigated the sensitivity of a behavioral model of microelectromechanical systems.

### Robust Design Methodology

Robust design methodology, often referred to as robust parameter design, is typically used in an industrial manufacturing capacity. Its purpose is to divide a set of parameters into two groups, a control group and a noise group, and determine which settings of the control parameters are optimal for minimizing response variation over the changing levels of the noise parameters. This is accomplished primarily through the investigation of control by noise interactions. The designs used in this methodology are termed cross arrays and are composed of two separate designed experiments. Most often, standard designs, such as fractional factorial, make up the cross array by creating a design for the control factors and running it for each experiment of the design from the noise factors. This requires $N$ runs where $N = n_{control}$ x $n_{noise}$. Analysis of this design consists of exploring the changing effects of the control parameters over the domain of the noise parameters. Additionally, changes in response variation are quantified and attributed to individual control parameters[1]. For an introduction to this method, see [202].

This type of experimental design was not found in the review of the literature as a method for sensitivity analysis of computer simulation models, however, similar method-

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[1] These are actually control by noise interactions.

ologies have been used in [141]. The robust design methodology is introduced here because it is used later in the sensitivity analysis of the individual model.

### 2.1.3 Response Surface Methods

In using DOE for sensitivity analysis on a computer model, approximating least squares linear models can be created. Many times, a linear model may prove to be an inadequate representation of the computer model. In these cases, quadratic effects for factors may need to be quantified. Response surface methodology is used to create designs for this purpose. For more information on response surface methodology, see [111].

Although not discussed in this section, note that full and fractional factorial designs with factors varied across more than two levels can be used as response surface designs. Some other response surface methods, which have not been found in the current literature as tools for sensitivity analysis of computer models and are not discussed here, are the Box-Behnken, non-central composite (sliding cube), and uniform shell designs.

#### Central Composite Designs

Central composite designs can be used as a next step in sequential experimentation once a resolution $V$ or higher design has been utilized. These designs are easily constructed by adding $2k + 1$ simulations to the original design, where $k$ is the number of parameters. This is accomplished by adding the center and axial points to the full or fractional factorial design and results in each parameter being varied across five levels. See [139] for details.

Central composite designs are discussed in [116]. In a study of a model of air scattered neutron dose from particle accelerators, the authors compared the use of a central composite design to a full factorial design at two levels for six factors [159]. Third-order orthogonal central composite designs were used to study the sensitivity of input parameters in plant growth simulation models [7]. A model of supply response of Australian broadacre farmers to four different input prices, each varying across five levels, was investigated using central composite design in [81].

## 2.2 Sensitivity Analysis of the Individual Model

Initially, Monte Carlo simulations with Latin hypercube sampling were used for the sensitivity analysis. Distributions of parameter values which were assumed to be normal were constructed. It was not known if parameters were correlated with one another, therefore, all pairwise correlations were assumed to be zero[2]. The measure that was used to detect a relationship between the model outputs of interest and each parameter was simple pairwise correlation. However, the results of this method did not prove to be useful. Accurate and consistent measures of relationships between individual parameters and the responses proved to be difficult to attain. Thus, a new sensitivity analysis technique which considered the possibility of parameter interaction was desired.

The technique chosen to perform a sensitivity analysis depends on the characteristics of the model being investigated: How many parameters are being considered in the

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[2] See [60, 178] for a discussion on why assuming zero correlation between parameters may not be a good assumption.

sensitivity analysis? How long does it take to run one simulation? Is it costly to run a simulation? Could interaction between effects be important? Does the possibility of quadratic or higher order effects need to be considered?

### 2.2.1 Isolation of Potential Sensitive Parameters

Ninety-five parameters were included in the initial screening sensitivity analysis of the individual model; twenty-two of these were known to be population level parameters (those associated with mortality), but were included in the sensitivity analysis of the individual model to verify that parameters which were known to not affect the individual model did not show up as sensitive. Note that all of the factors in the model considered here are continuous, not categorical. The initial values used for each parameter were either found in the literature or created, as noted in Tables 1-6. These nominal values are referred to as the "mean" level for each parameter. Associated with each parameter value is also a standard deviation, taken from the literature when available and otherwise set to ten percent of the mean value. One exception to this rule was the standard deviation for parameters that had dimensions of [days]; these parameters had standard deviations set to values of either 1.0 or 10.0. The standard deviation is the base value that is added or subtracted from the mean value in order to run an experiment at either its high (+) or low (-) level, respectively.

There were a few exceptions to this set-up. Some parameters were already set at either their lowest ($aa$, $spwn1$, $rmfec$, $aal$, $migl1$, $aao$[3]) or highest ($bb$, $spwn2$, $bbl$, $bbo$)

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[3] The names of the parameters given here are the names used in the code.

possible levels, and, therefore, were not allowed to go beyond the values set as either a minimum or a maximum. In order to induce changes across low and high levels for the sensitivity analysis, the means were readjusted such that the extreme values would not be exceeded. Parameters $a5$ and $a6$ were handled in a similar manner to satisfy the condition $a5 \leq a6$.

The final exception to the mean values and standard deviations used included the parameters related to temperature modification (see Table 4), which were found, in most cases, by fitting a non-linear function to data from the literature (see Appendix II). Instead of associating a standard deviation to each of the parameters which made up the function, a surrogate parameter was created to allow the function value to change across low and high levels. The surrogate parameter had a mean value of 1 (when the function was evaluated at the base case, the multiplier was 1 so the value of the function did not change) and a standard deviation of 0.1. For example, instead of varying the parameters ($fkopt$, $falpha$, $ftopt$, $fthigh$) in the function which describes how temperature affects feeding, $f_2(T)$, a new parameter, say $\chi$, was created which modified the value of $f_2(T)$ such that the new value was $\chi \cdot f_2(T)$. The functions associated with the temperatures in the lake and ocean environments which were determined by the time of the year were also modified in this fashion.

The preliminary sensitivity analysis demonstrated that interaction between effects existed and the extent to which they could be considered negligible was questionable. The decision about the importance of higher order effects were made during sequential experimentation. Depending on how the parameters were varied, one simulation of the individual model with only one ecotype took approximately three to five seconds. There were no costs associated with running the model, other than the time invested. Taking this into consideration, if the time it took to run one designed experiment versus another was only a difference of a few hours, the experiment which would yield more conclusive results was chosen because the simulations were usually run overnight. Therefore, if the costs associated with running a model were greater than those here, the number of simulations could easily be reduced[4].

To try to eliminate the possibility of failing to identify a parameter that had an effect on the output variable over a small part of its domain, as well as to identify any nonlinearities and/or thresholds in the effects of the parameters, varying levels of high (+) and low (-) were implemented. The levels used were obtained by multiplying the standard deviation of the particular parameter by ± 0.01, 0.05, 0.10, 0.25, 0.50, and 1.0.

The model outputs used as forecast variables were the total mass of an individual, $m_L + m_S$, at the beginning of Stages 2, 4, and 6 (see the discussion on Migration in Section 1.2.1), the number of eggs produced, and the age at reproduction. Hereafter, the forecast variables will be referred to as $Mass$ 1, $Mass$ 2, $Mass$ 3, $Eggs$, and $Age$, respectively. The idea behind the sensitivity analysis was to not only find to which parameters the forecast variables were sensitive, but also to be able to adjust the

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[4] The number of simulations could have been further reduced by excluding the additional population parameters which were included for reasons previously stated.

parameter values within their ranges such that the forecast variables would be within realistic ranges of values. The following ranges of values from the literature were used as goal values:

$Mass$ 1: 0.70-1.74 grams (dry)[5] [64]

$Mass$ 2: 600-1200 grams (dry) [88]

$Mass$ 3: 410-830 grams (dry) [62]

$Eggs$: 1500-5500 [62]

$Age$: 1095-1460 days (3-4 years)[6] [28]

Once the sensitive parameters were known, they were then used to construct a population of different individuals, all with reasonable forecast values.

The statistical package JMP® [107] was used to create some of the designs that were implemented in the sensitivity analysis. JMP® is able to generate screening designs, Cotter designs, response surface designs, Plackett-Burman designs, and many others that were not utilized here. The response surface design is limited to eight factors. JMP® is not able to create the saturated resolution $V$ design, however, this design can easily be generated by hand (see [160]). The Fit Model platform was used to analyze the model output associated with the designed experiments.

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[5] The value for the mass given here is for smolt migration taking place in the first year.

[6] The possibility of non-fourth year migrants was not excluded, however, it is accepted that Fraser River sockeye typically migrate in their fourth year.

### Resolution $III$ and $IV$ Designs

The sensitivity analysis was begun with a resolution $III$ screening design. For a complete picture of the sequential experimentation implemented, see Figure 2. The intent was to estimate main effects in a general screening procedure, however, higher resolution designs were sequentially performed in an effort to identify main effects clear of interaction terms. Models of the main effects from the resolution $III$ design which was folded over into a resolution $IV$ design had high coefficients of determination ($r^2 > 0.8$), however, validation of these models was completely unacceptable. Similarly, residual plots showed groupings of data not explained by any estimable effects. These poor model qualities were attributed to possible interaction effects.

### Saturated Resolution $V$ Design

Following the initial screening designs, a saturated resolution $V$ design was run on all 95 factors in 4,561 runs. These models become extremely inefficient with respect to estimating precision with so many factors, however, due to the deterministic nature of the responses, this was not an issue. The results of this design were again confusing, as models of main effects could not be validated. Significant main effects were judged not through statistical tests but subjectively through the magnitude of the estimates. One reason for this was because the estimate of error, $\sigma$, measures not random error, but variation due to missing terms in the model. When judging for significant main effects, there was not a clear cutoff in the magnitude of effects. Since this design had higher order interaction effects confounded with the main effects, it began to be hypothesized that estimates for main effects may in many cases be caused by the additive effects of several small higher order interactions. This design was folded over to create a resolution $VI$ design in an effort to clear additional higher order interactions (four-factor) from the main effect estimates. Results did not change significantly and no final conclusions could be drawn[7].

### Cotter Design

The next design implemented in this series of sequential experiments was a Cotter design, which required 192 runs. The Cotter design is not used to build models, but to estimate the sums of odd order effects and the sums of even order effects for which each factor is involved. Included in the estimate of odd order effects is the main effect for each factor. In analyzing this design, it was found that the sums of even order effects were, for many factors, just as large or even larger than the sums of odd order effects. These results further backed the emerging hypothesis that there were many somewhat significant interactions between the parameters.

### Results of Screening

As an approach to factor screening, reverse methodology was used in that, instead of screening for significant factors, screening for insignificant factors was employed.

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[7] Future references to the saturated resolution $V$ design actually refer to the results of the folded over design.

To accomplish this, the results of the saturated resolution $V$ design and the Cotter design were combined. The estimates of main effects from the resolution $V$ design were compared to the sums of odd order effects from the Cotter design. It is reasonable to assume that, since these designs have different alias structures, if a factor showed very little effect in the resolution $V$ design and also showed a low sum of effects in the Cotter design, then the main effect for that factor was most likely small. On the other hand, if a factor estimate was large in either or both designs, then it was cause for further investigation.

This type of analysis is demonstrated in Figure 3 where the resolution $V$ and odd Cotter estimates for $Mass$ 2 and $Eggs$ are plotted against one another[8]. Note that the circled points showed little or no effect, having estimates close to zero, in both the Cotter and resolution $V$ designs. Therefore, the parameters associated with these points were assumed to have little or no effect on the forecast variables, $Mass$ 2, $Mass$ 3, and $Eggs$. Thus, by eliminating the insignificant factors, the possible significant factors remained: $a0l$, $a3$, $a4$, *oplx*, $a0p$, $a6$, $k1$, *cg*, *oppx*, *obdensp*, and the surrogate parameters associated with temperature in the lake and ocean environments, which will be respectively referred to as *templ* and *tempo*.

The $Mass$ 1 output, the mass at time of migration from the lake environment, was found to be most sensitive to the parameter *mmigl*, which is the minimum mass that must be reached in order for migration from the lake to take place.

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[8] The plot for $Mass$ 2 is only given here due to the strong correlation between $Mass$ 2 and $Mass$ 3 with both plots appearing very similar.

The parameters to which the *Age* output was sensitive were difficult to determine. The results of the screening analysis indicated that *Age* was most sensitive to eight parameters (*a0l*, *a3*, *a4*, *oplx*, *zjmgl*, *blsp*, *bdensp*, *ppx*), however, these parameters, their interactions with each other, and their interactions with other parameters also appeared to be important. In trying to validate the effects of these parameters on *Age*, consistent measures of the relationship were not found. Since *Age* was within the realistic range of values and appeared to be determined by the physiology of the individual, further sensitivity analyses on this output were not conducted.

### 2.2.2 Investigation of Potential Sensitive Parameters

Once the possible sensitive parameters were identified, the next step was to look at the effects of these parameters on the forecast variables in more detail. Sequential experimentation was again utilized to achieve this goal.

#### Central Composite Design

A $2^{12-2}_{VIII}$ fractional factorial design combined with the center and axial points resulted in an orthogonal central composite design which was implemented in $n = 1049$ runs. All non-sensitive parameters were kept at their mean levels.

It was found that across the responses, only eight of the parameters had large effects (see Table 8). The same seven parameters were influential for each of the responses, with *Eggs* having the additional important parameter *templ*. Despite eight parameters being listed as highly sensitive for *Eggs*, it should be noted that *templ* is extremely influential compared to the other parameters shown for this response. Also listed in Table 8 are the parameters for which the responses were somewhat less sensitive than those previously mentioned[9]. These "slightly significant" parameters influenced the forecast variables, but were not capable of causing extreme changes as were the highly significant parameters.

The analysis showed that there were small interaction effects and slight curvature in several of the parameters. As previously stated, an advantage of using DOE for sensitivity analysis is the ability to create parsimonious approximation models for the responses. In this case, good approximation models were created over parts of the domain, however, due to nonlinearities and thresholds, these models could not be used as global approximations. This further supports the need for the complex individual-based model implemented here based on the physiology of the individual.

### Robust Design Methodology

Having identified the parameters to which the responses were most sensitive, it was also important to determine whether the interaction effects of other non-sensitive parameters with the important eight were large enough to be of practical concern. To accomplish this, robust design methodology was employed. A cross array was created using an orthogonal $2^{8-4}$ fractional factorial (plus one center point) for the eight important parameters and, an 88-run, Plackett-Burman design for the remaining 87 parameters. The

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[9] Some parameters appearing in Table 8 have not been indicated as sensitive thus far, but will be discussed in the following subsection.

total number of simulations was $n = 1496$. Through this design, insight into the changing effects of the eight parameters was gained by running the $2^{8-4}+1$ simulations at 88 different locations within the design space. The standard deviations of the runs in each Plackett-Burman (i.e., at each point in the $2^{8-4}+1$ design) were modeled to determine if any of the eight important parameters were involved in significant interactions with any of the other 87 parameters.

In the analysis of this cross array, it was found that parameters *oppx*, *obdensp*, $k1$, and *templ* were all involved in interaction effects with other parameters with respect to $Mass$ 2 and $Mass$ 3. It was also found that five other parameters, *zjmgl*, *zjmgp*, *blsp*, *bdensp*, and *resvar*, also had slightly significant effects or were involved in interaction effects with significant parameters. However, the extent of these interaction effects was not large enough to cause concern.

### Results of Sensitive Factor Analysis

Through the use of sequential and combined experimental designs, it has been determined that there were eight parameters to which the responses were extremely sensitive and nine more to which the responses were less sensitive. Given the extreme sensitivity of the parameters listed in the first column under each response in Table 8, all of the highly sensitive parameters, with the exception of *templ* which was not adjusted, were set to appropriate values (see Tables 1-6). Four of the slightly sensitive parameters ($a0l$, $a3$, $a4$, *oplx*), in combination with the level of resource, were chosen to add variability to the individuals in the population. For easy reference, each ecotype is assigned a number in Table 9.

Although more sequential experimentation was used than was originally thought to be needed, the total number of simulations performed was still small considering the resulting thoroughness of the sensitivity analysis. In comparison to the one-factor-at-a-time method, the DOE approach is more systematic, efficient and thorough. The potential problem of changing relationships over the domain as previously discussed can lead to erroneous results with one-factor-at-a-time methods whereas the DOE methods employed here safeguard against this problem. The use of sequential experimentation allows the result of each experiment to guide succeeding experiments to achieve a conclusive result. While DOE methods have been used as methods for sensitivity analyses as noted in the literature, the sequence and combination of designed experiments and the use of reverse methodology here was a new and innovative approach.

## 2.3 Sensitivity Analysis of the Population Model

Twenty-five parameters were included in the sensitivity analysis of the population model. All of these parameters were associated with mortality, with the exception of *idiv*, and are listed in Table 6. Starting with a population of 243 different ecotypes resulted in one simulation of the population model taking approximately ten to fifteen minutes. Again, the only cost associated with running the model was the time invested. Given no reason to assume otherwise, the assumption that interactions between main effects were negligible was made.

A $2^{25-18}$ resolution $IV$ design was implemented in 64 simulations. The output that was analyzed was the average number of individuals over forty years or the lifetime of the whole population, whichever occurred first, for values sampled the 30th day of each month. There was no predetermined range of values in which this forecast variable was supposed to fall; the idea was to find the sensitive parameters and be able to adjust them by a small amount such that extinction of the population was in general avoided allowing for the population dynamics to be studied.

The results of this designed experiment were much more clear than the individual model results. The following parameters, listed in order from most to least, were found to be sensitive: $zmuw$, $zmuv0$, $zmuvf$, $yoymort$, and $zmua$. The first four of these parameters were adjusted by two standard deviations in the negative direction to achieve the desired result.

The sequential experimentation used for the individual-based model together with the fractional factorial design implemented for the population model illustrates the flexibility of the DOE method. Both started out with the same type of screening experiment; the desired result was immediately achieved for the population model, whereas in the case of the individual-based model, further sequential experiments were required.

# Chapter 3

# Simulation Results

## 3.1 Diversity

In general, diversity is a measure which represents how many different types of organisms are present (richness) and how different the relative abundances of those organisms are (evenness) [150, 152]. Specific to the sockeye salmon model studied here, diversity of the population (i.e., number and type of ecotypes remaining) after a steady state was reached was an output of interest.

Combinations of simulations which varied across different levels of lake resource ($resource$) and maximum possible number of schools ($idiv$) were carried out. The starting point for each simulation, other than the variation in the resource levels, was the population consisting of 243 ecotypes described in Section 2.3 (see also Table 9). Each simulation was run for 2000 years, which allowed for a limit cycle to be reached in all but two cases.

As is evidenced by Table 10, varying the maximum possible number of schools under different resource conditions had an effect on how many ecotypes survived as well as which specific ecotypes survived. The number of ecotypes remaining as a result of these simulations, which were run until a steady state was reached, unless specified otherwise, varied between zero (extinction) and six, however, the most prevalent number of ecotypes remaining was between one and four. The specific surviving ecotypes, characterized by the values of $oplx$, $a0l$, $a3$, $a4$, and $resource$, can be cross referenced with Table 9.

## 3.2 Cycles and Cyclic Dominance

Cycles and cyclic dominance in salmon populations are phenomena which have been widely noted in the literature [54, 134, 165, 167, 192]. As defined in [167], a cycle is a sequence of $x$ lines in successive calendar years, where $x$ is the principal age at maturity of the population under consideration. (For Fraser River sockeye, $x = 4$.) Cyclic dominance means that within the $x$-year cycle, there is one year in which the number of returning spawners greatly exceeds the numbers in the other years. This year is referred to as "dominant" and the other years are called "off" cycles. When the year following the dominant one is "close"[1] to the dominant year in terms of abundance, it is referred to as "subdominant". The dominant year is placed in the first position of the cycle and is denoted Cycle I. The subdominant and off years, for a four-year cycle,

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[1] 10-25% of the value in the dominant year, as per [167].

are then Cycles II, III, and IV, respectively.

It has been suggested that the sharp decline in the abundance of Pacific salmon populations since the early 1990s has been due to a combination of factors which primarily include climate change, overfishing, and freshwater habitat destruction [119, 146]. Prior to this decline, it was an important challenge to be able to explain the cycles which appeared, but even more so now that population numbers are dwindling. If the resulting explanation involves factors which can be controlled, it may be possible to manipulate the factors to boost the abundance of the salmon populations in all cycle years.

### 3.2.1 Proposed Cycle Mechanisms

Many explanations, arrived at through examining data and using simple population models, have been proposed to explain the occurrence of the cycles seen in some salmon populations. (Reviews can be found in [126, 167, 192].) In the discussion that follows, the terms "compensatory", "depensatory", and "extrapensatory" are used. These three classifications of the mortalities that affect salmon populations were introduced in [145] and respectively mean mortalities that are directly density-dependent, mortalities that are inversely density-dependent, and mortalities that are independent of the population density[2].

First note that it is widely accepted that Pacific salmon cycles and cyclic dominance are a result of some mechanism which occurs in the freshwater environment [37, 126,

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[2] In the literature reviewed, extrapensatory mortalities were typically associated with environmental factors.

134, 145, 165, 192]. The possibility that the cycles came about due to interactions in the marine environment was not considered specifically due to a study of salmon in the Fraser River system in [165, 192]. Ricker found that marine influences could not have generated the asynchronous cycles observed for different races within the Fraser River system, and, therefore, the cycles must be a result of some mechanism occurring in the freshwater environment.

Additionally, it was suggested in [192] that cyclic dominance is occurring due to some type of depensatory mortality acting on Cycles II, III, and IV in comparison to Cycle I. If the mortality was not depensatory, the abundances of the off years would likely be the same level as the dominant population. However, there is no empirical evidence which supports this claim [58, 164, 165].

Some authors tried to demonstrate that delayed density-dependent mortality[3] was the cause of the Pacific salmon cycles [37, 42, 121, 122, 126, 165, 167, 191, 192]. Examples of mechanisms which could induce delayed density-dependent mortality were competition (the large abundance of smolts in the dominant year having an effect on the abundance or composition of the resource available to juveniles in subsequent years) and predation (disease, parasites, or predators are built up during the dominant year and result in a higher mortality rate for the off years). While delayed density-dependent mortality can reinforce cycling, it has not been demonstrated that it is actually needed to generate the cycles [143, 144], and in some cases, has not been supported by field sam-

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[3] Examples of both compensatory and depensatory mortality were found.

pling [165, 192, 200]. Cycles were recreated in the absence of delayed density-dependent mortality, where depensatory mortality was used instead, in [144]. The results of the studies in [143, 144] imply that a reduction in fishing mortality in the non-dominant years could bring about an increase in abundance.

A genetic factor was suggested as being partially responsible for the existence of the salmon population cycles in [190]. The genetic factor referred to is the age at maturity for the different lines in the population, which is determined in part by heredity and in part by environmental conditions. The authors hypothesized that the cycles could be explained by this genetic factor in combination with high fishing mortality rates. To prove their hypothesis, the authors incorporated age four and five spawners into a population model with density-dependent effects and demonstrated that the number of age five spawners in the population adversely affected the off-cycle lines in the four-year cycle. This explanation for the appearance of the cycles was refuted in [167] where it was shown that the occurrence of age five fish in the population tends to increase the population numbers in the off years. While the authors in [122] recognized that age at maturity is in most cases the same for parents and their progeny, they believe that this factor alone cannot explain cyclic dominance. Genetic factors, in general, were suggested and then dismissed as a possible reason for cyclic dominance in [192] where the authors sought to find an explanation for cyclic dominance in some other factor, such as predation, competition, or fluctuations in resource availability.

Another reason for the appearance of the cycles that has been posed is depensatory fishing, or fishing mortality that is inversely related to abundance [41, 58, 126, 149]. Depensatory fishing may enhance the natural tendency of the population to cycle at a period equal to the age at maturity, but the cycles still existed in its absence [37, 126, 144, 167]. The authors in [37, 192] also pointed out that it is unlikely that the aboriginal and early commercial fisheries were intensive enough to sustain the cycles that existed prior to 1860.

### 3.2.2 Cycles in the Model

As the simulations for analyzing the diversity of the population were carried out, a pattern in the total number of individuals returning to the lake to spawn each year was discovered. The pattern identified was a cycling of the total number of returning individuals with a period of 4, 12, 16, or 20 years. The period of the cycle was determined by whether or not reproduction (by any number of ecotypes) took place in each year of a four year time span: if reproductions only occurred during one of the four years, then the periodic cycle was four years long; if reproductions occurred during two of the four years, the periodic cycle was 12 years; if reproductions occurred during three of the four years, the periodic cycle was 16 years; and finally, if reproductions occurred every year in the four year period, the periodic cycle was 20 years.

These different length cycles (4, 12, 16, and 20) encompass all the possibilities for reproductions which can take place in a four year period, i.e., there are $\binom{4}{1} + \binom{4}{2} + \binom{4}{3} + \binom{4}{4} = 15$ possible ways that reproductions can occur each year in a four year period and each is represented in one of the cycles described. Within a four year period ($- -$

$- -$), if reproductions are denoted by "+", each of these possibilities can be illustrated. Reproductions in a single year within a four year period would be one of

$$\begin{array}{cccc} + & - & - & - \\ - & + & - & - \\ - & - & + & - \\ - & - & - & +. \end{array}$$

If we look at each of these four year periods as a repeating pattern, then each set has the same basic form, but the year in which reproductions take place is translated. All of these reproduction patterns result in a four-year periodic cycle.

Reproductions occurring in two out of four years would have one of the following patterns:

$$\begin{array}{cccc} + & + & - & - \\ - & + & + & - \\ - & - & + & + \\ + & - & - & + \\ + & - & + & - \\ - & + & - & +. \end{array}$$

The first four of these patterns all have the same basic form with reproductions translated to a different set of consecutive years; similarly, the last two patterns have the same form with reproductions translated. Each of these patterns results in a 12-year periodic cycle.

Reproductions occurring in three out of four years result in four possible patterns:

$$\begin{array}{cccc} + & + & + & - \\ + & + & - & + \\ + & - & + & + \\ - & + & + & +. \end{array}$$

All of these are of the same form, with the one year in which reproductions do not occur being translated. A 16-year periodic cycle results here.

There is only one possible pattern for reproductions occurring in all four of four years:

$$\begin{array}{cccc} + & + & + & +. \end{array}$$

This pattern results in a 20-year periodic cycle.

Although each of these patterns demonstrated a distinct cycling, each could also be regarded as a four-year cycle. The values which appeared every fourth year in each of the 12, 16, and 20 cycles could be considered essentially the same number because the coefficient of variation ($CV$) ranged from as little as 0.1% to at most 4%, with an average of 0.15%.

Given that the population model resulted in periodic four-year cycles and that the Fraser River system sockeye populations tend to have cycles of four years, a qualitative comparison of the model output and data from Cultus Lake for the number of returning spawners was conducted. Yearly data for the number of returning spawners at Cultus Lake were available for the years 1956 through 1988 in [54], however, data from 1956, 1957, and 1958 were not included since the four-year dominant cycle value (1955) was not available. Considering that the number of returning spawners for this lake was positive for all years reported, the data were compared to the 20-year cycle model output, which had individuals returning in every year of the four year period. In Figure 4, every year of the data extracted from [54] was normalized by the first value in the time series and plotted against the model output, which was also normalized by the value of the first year in the 20-year cycle. As demonstrated by Figure 4, the qualitative comparison of the data to the model output was lacking. However, taking into account that the historical data have been interpreted as a series of four-year cycles, an adaptive fitting scheme in which the data were renormalized every four years by the value associated with the dominant cycle was used and yielded much better results[4]. See Figure 5. Although the model output did not have as dramatic changes as the historical data, the qualitative behavior was essentially the same: starting with a dominant year, both graphs show a sharp decrease, another decrease, and then two increases (DDII) returning back to the dominant year.

While the four-year cycles which resulted from the model may seem to be an obvious outcome, one must realize that a value of four for the age at maturity was *not* programmed into the model. The resulting age at maturity was a consequence of the

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[4] All years in the 20-year cycle from the model were still normalized by the first value given the previous discussion on the $CV$s associated with every fourth year.

physiology of the individual. It is possible to have individuals which mature at ages other than four.

Other systems, such as the Kvichak River in Bristol Bay, Alaska and the Skeena River in British Columbia, have sockeye populations which grow slower and hence migrate and mature at different ages than those of the Fraser River system. For example, in the Kvichak River system, individuals migrate from the freshwater environment in their third year and mature primarily at age five [58, 134]. Simulations using a slower growth rate were executed by adjusting some parameter values associated with individual growth. Different cycles appeared as the size-based mortality value, $zmuw$, was varied, however, the primary age at maturity in all the simulations was five years with an age at maturity of six years appearing sporadically.

In all of the simulations executed in which there were only ecotypes maturing at an age of five years, the resulting cycles had periods of five, 15, 20, 25, and 30 years. When reproductions took place in only one of these five years, the result was a five-year cycle. When reproductions occurred in two of five years, a cycle with a period of 15 years resulted. When reproductions occurred in three of the five years, cycles of 20, 25, and 30 years were all found. There were no cases in which reproductions took place in four and five out of the five years, however, this does not imply that they do not exist. The simulations in which an age at maturity of six years appeared even once, in combination with the number of reproductions taking place each year in the five year period under a particular schooling condition, potentially caused the cycles to have a longer period.

### Mortality Effects

The models used to describe the effect of mortality mentioned at the beginning of this section were population-level models, not individual-based models incorporated into a population model. These models, by necessity, only assessed mortality as a form of density dependence. In this setting, it was not possible to independently impose a density-dependent mortality and a size-dependent mortality because all of the organisms being modeled were exactly the same; in other words, size-dependent mortality would have been equivalent to density-dependent mortality.

In the model framework used here, both density- and size-dependent mortality can be imposed separately, as illustrated in Appendix III. Since the form of the density-dependent mortality was not of a delayed nature and it was demonstrated in the previous section that cycles do exist, the model is in agreement with the results found in [144] in that delayed density-dependent mortality was not necessary to generate the cycles. The hypothesis that the cycles were a result of some other type of mortality is considered in the text that follows.

**Density-dependent Mortality** To ascertain if density-dependent mortality was the cause of the cycles which appeared, the effect of removing this type of mortality from the model was examined. Once removed, it was found that cycles still occurred. Under the original resource level conditions (those listed in Table 1), both 16 ($idiv$ = 6, 12) and 20-cycles emerged ($idiv$ = 3-5, 7-11). Extinction occurred for $idiv$ values of one and two. The $CV$ across all the simulations for the values occurring every four years was, however, much greater than when density-dependent mortality was included; the average was 4%, with a minimum of 0.25% and a maximum of 14%. This result indicated that under some schooling conditions, the emerging pattern could not be interpreted as a four-year cycle as before. While the age at maturity for all of the surviving ecotypes for each of the simulations was still four years, the maximum possible number of schools chosen and the absence of the density-dependent mortality did affect the length of the period of the resulting cycle.

When the maximum possible number of schools was three, i.e., $idiv = 3$, the same type of pattern as when density-dependent mortality was present arose (see Figure 6). The cycles which emerged in the absence of density-dependent mortality followed the same DDII pattern within a four year period, having an average $CV$ of 0.28%. However, the cycles produced in the absence of density-dependent mortality were not as pronounced as those when it was included. The reoccurring DDII pattern previously found within the 20-cycle was not generated under other schooling conditions. For the rest of the 20-cycles produced, there were four surviving ecotypes, each reaching maturity at an age of four years, never in the same year as another ecotype. Based on their $CV$ values, the resulting 20-year periodic cycles could not be considered four-year cycles. However, for the simulations associated with a maximum possible number of schools of three, five, seven, and eleven, every year could be considered a dominant year given that the maximum $CV$ for these four simulations for all the years in the 20-year cycle was 1.9%.

While the same pattern of the four-year periodic cycle found previously was only recreated under one schooling condition here, the fact remains that cycles did appear when there was no density-dependent mortality. The overall effect of including density-dependent mortality caused the magnitude of the cycling pattern to be more dramatic. Excluding density-dependent mortality did not eliminate the cycles, but had the potential to change their character.

**Size-based Mortality** An alternate hypothesis was that size-based mortality caused cycling to occur. If this type of mortality was taken out of the model, and density-dependent mortality was left at its original value of 0.002, extinction occurred under the range of allowed values for the maximum possible number of schools (*idiv*). The reason for this extinction was, in effect, that the other mortalities, in particular the density-dependent mortality, did not eliminate enough individuals in the freshwater environment to allow migration to take place. Due to the greater number of individuals in this setting, the resource was partitioned to a greater extent, which, in turn, caused each individual to grow much slower. This slow growth caused the threshold for the minimum mass to migrate not to be attained within the specified time period. Essentially, the individuals were not getting sufficiently large to leave the freshwater environment, causing them to die when the prescribed maximum age was reached. No conclusions about whether or not size-based mortality was causing the cycles to occur could be made under these conditions, therefore, density dependent mortality was increased, while excluding size-based mortality, to reduce the population in the freshwater environment, allowing migration from the lake to occur.

Once the density-dependent mortality values were increased, it became clear that cycles could also exist in the absence of size-based mortality. Simulations under the original resource levels were conducted for *zmudm* values of 0.006 and 0.007 across the plausible range of *idiv* values.

For a *zmudm* value of 0.006, two different cycles emerged. The first pattern which presented itself, a six-year cycle which had reproductions occurring in only one year of the six-year period, was for *idiv* values of one and four. The age at maturity for all individuals in this cycle was six years. The second pattern which arose was a 64-year cycle when the maximum possible number of schools was two. When the steady state was reached, there was only one ecotype left. This ecotype and its offspring both reached maturity after six years; the third generation matured at seven years, the fourth at six years, the fifth at seven years, and then the pattern repeated. This cycle could be interpreted as a 32-year cycle given an average $CV$ of 0.0023% for the values being produced every 32 years at the different maturity ages. Extinction occurred for *idiv* values of three and five through twelve.

When the value for the density-dependent mortality was increased to 0.007, extinction again occurred for the majority of *idiv* values (2-5, 7, 8, 10-12). For one school, a 74-year cycle was generated with two ecotypes surviving. All generations of spawners included both ecotypes. The first generation returned to the lake after seven years, the next generation after six years, then seven years, four years, six years, and seven years, after which time, the pattern repeated. The average $CV$ of 0.44% for the values appearing every 37 years indicated that this cycle could be interpreted as a 37-year cycle. A 108-year cycle emerged when *idiv* was set to six. Two ecotypes survived, each reaching maturity at an age of six, with reappearance in the lake offset by an interval of two years. This cycle could be interpreted as two six-year cycles with a delay of two years between each. One ecotype survived when the maximum possible number of schools was nine, resulting in a 120-year cycle. This ecotype returned to spawn every six years. The cycle produced could be interpreted as a six-year cycle given that the $CV$ was 0.58%.

The conclusion drawn from taking a closer look at these two types of mortality, density-dependent and size-dependent, was that their inclusion was not necessary for periodic cycles to appear. However, in combination with the value chosen for the maximum possible number of schools, both of these mortalities did have an effect on the character of the periodic cycles. In analyzing all of the simulations executed, it became clear that the long term behavior of the population was extremely sensitive to the dynamic nature of the schools and their effect on the initial population.

# Chapter 4

# Future Directions

The sockeye salmon model implemented here was used in a number of different ways, the most obvious application being the study of the dynamics of the population. In addition, the validity of some hypotheses regarding the cycling of the populations which appear were examined, and, a new sensitivity analysis method was tested and found to be an efficient and thorough tool. Some possible future directions for the work completed here are discussed in this chapter.

## 4.1 Schooling Mechanisms

The creation of schools in the freshwater environment used in this model was discussed in the schooling section of Section 1.2.1. It was found that the maximum possible number of schools allowed in each simulation, given by the value of $idiv$, had a significant effect on the type of cycling which resulted. Since the mechanism behind how many schools any given group of fish will form and how many fish will be contained within a school is not known, other ways of creating schools in the model are certainly possible and should be explored. For example, perhaps a limit to the number of fish that form a school exists. If this is the case, once a school has reached its capacity, a new school with individuals of the same length as the school which is "full" could then form, resulting in an increase in the total number of schools as well as a change in the density of the individual schools. The maximum number of individuals associated with a school might also vary between schools containing individuals of different lengths. Likewise, some minimum number of individuals above one might also be necessary for a school to form at all.

## 4.2 Dynamic Resource

The resource that was used in both the freshwater and ocean environments in the implementation of the model was set at a constant density such that it was not possible for the organisms to deplete the resource. While conditions which did not limit feeding were reasonable for the ocean environment [57, 176, 182, 189], making this assumption in the freshwater environment is questionable. The inclusion of a dynamic lake resource which can grow and be reduced when consumed is a logical next step for improvement of the model. Given a resource which fluctuates in response to its environment, the hypothesis presented in [110] in which it is suggested that smolt migration is in part a response to low resource levels could be investigated.

## 4.3 Toxicological Problems

One of the problems that some populations of salmon encounter is pollution in the environments in which they live [119]. The inclusion of lipid as one of the state variables allows for problems associated with many toxic chemicals to be studied. The model implemented here, with a few minor modifications, is equipped to examine scenarios in which toxicological problems could be addressed. The effects of toxic chemicals on other species using the same type of model formulation were investigated in [83, 128].

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# Appendices

# Appendix I

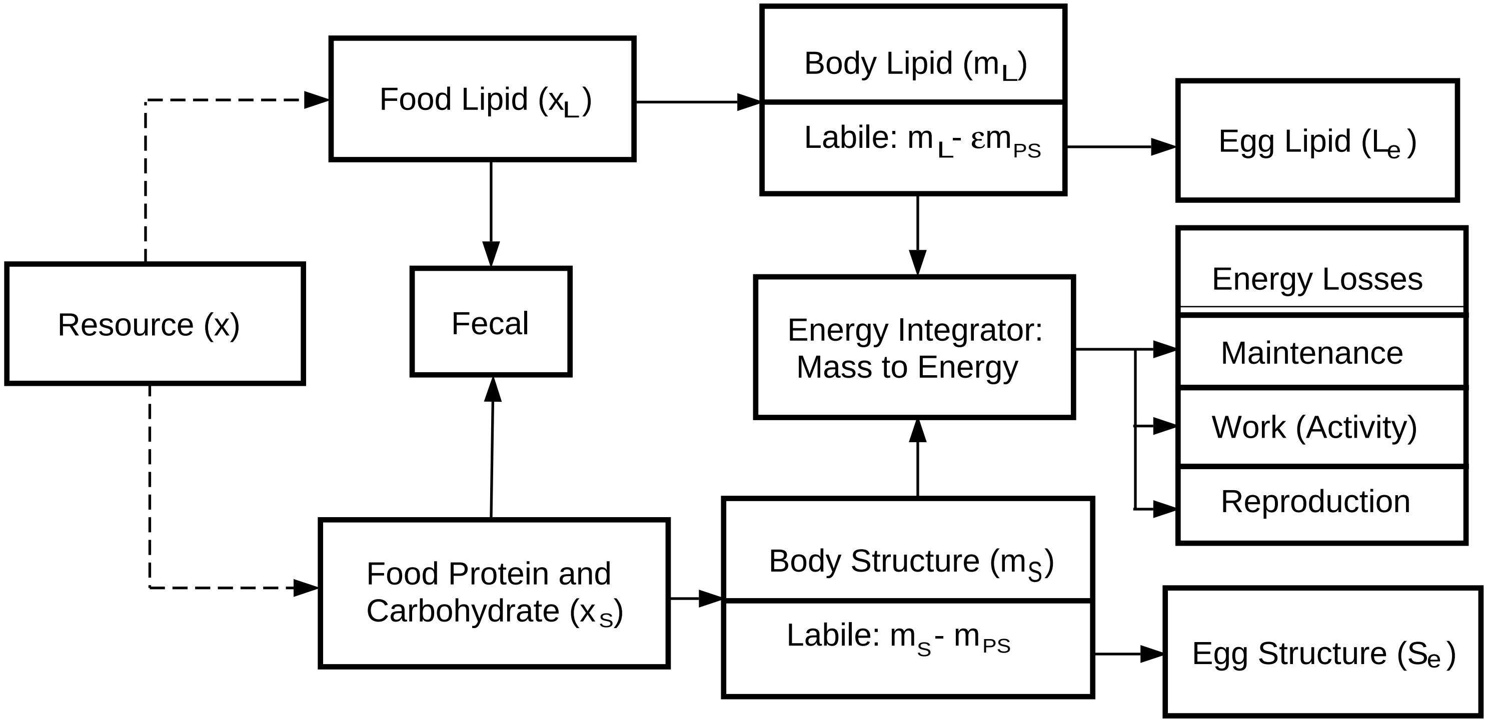

**Figure 1. Flow diagram for energetics of an individual female fish.**

Table 1: Description and values of general parameters and parameters related to structuring the population. All weight values are dry weights.

| Variable Name |  | Value | S.D.[a] | Units | Description | Notes | Reference |
|---|---|---|---|---|---|---|---|
| In Text | In Code |  |  |  |  |  |  |
| **Parameters related to structuring the population** |  |  |  |  |  |  |  |
| $A_{0L}$ | a0l | 0.85 | 0.05 | [ ] | Assimilation efficiency for lipid | Values used: 0.759, 0.8045, 0.85 | [10, 70, 174, 199] |
| $A_L$ | a3 | 0.12 | 0.012 | $\frac{1}{d}$ | Labile lipid mobilization rate constant | Values used: 0.09816, 0.10908, 0.12 | [19][b] |
| $A_S$ | a4 | 0.37 | 0.037 | $\frac{1}{d}$ | Labile structure mobilization rate constant | Values used: 0.37, 0.40367, 0.43734 | [19][b] |
| $x$ | resource | 0.00000012 | 0.00000006 | $\frac{g}{cm^3}$ | Density of resource in the lake | Values used: 0.00000006, 0.00000012, 0.00000018 | [162] |
| $\frac{x_L}{x}$ | oplx | 0.173 | 0.0173 | [ ] | Fraction of lipid in resource | Values used: 0.141514, 0.157257, 0.173 | [94] |
| **General fish-related parameters** |  |  |  |  |  |  |  |
| $\beta_f$ | beta1 | 0.013 | 0.003 | $\frac{g}{cm^3}$ | Allometric mass/length coefficient |  | [38, 72, 168] |
| $\beta_2$ | beta2 | 0.4 | 0.04 | [ ] | Allometric surface area/length coefficient |  | [198] |
| $q$ | q | 0.2 | 0.02 | [ ] | Swimming efficiency |  | [198] |
| $\epsilon$ | epsilon | 0.11 | 0.065 | [ ] | Ratio of nonlabile lipid to nonlabile structure |  | [33][c] |
| 38940 | zjmgl | 38940.0 | 3894.0 | $\frac{J}{g}$ | Energetic content of lipid |  | [74, 104] |
| 17170 | zjmgp | 17170.0 | 1717.0 | $\frac{J}{g}$ | Energetic content of structure |  | [74, 104] |
| $A_{0S}$ | a0p | 0.722 | 0.0722 | [ ] | Assimilation efficiency for structure | Adjusted value = 0.67507 | [6][d] |
| $B_L$ | a3zero | 0.0069 | 0.00069 | $\frac{1}{d}$ | Value of a3 before feeding occurs |  | [180][d] |
| $B_S$ | a4zero | 0.02 | 0.002 | $\frac{1}{d}$ | Value of a4 before feeding occurs |  | [14], [180][d] |
| $\alpha_1$ | a5 | 0.73 | 0.05667 | [ ] | $m_{PS}$ coefficient for starvation level | a5 must be $\leq$ a6,<br>Set to a6 value = 0.7668355 | [33] |
| $\alpha$ | a6 | 0.73 | 0.05667 | [ ] | $m_{PS}$ coefficient | Adjusted value = 0.7668355 | [33] |
| 32.9 | a7 | 32.9 | 6.5 | $\frac{J/g}{d}$ | Energy to maintain 1 g of lipid |  | [8], [27][c]; [30][e] |
| 32.3 | a8 | 32.3 | 6.5 | $\frac{J/g}{d}$ | Energy to maintain 1 g of structure |  | [8], [27][c]; [30][e] |
| $s_c$ | blsc | 4.0 | 0.4 | $\frac{1}{s}$ | Body lengths per second of fish in pursuit |  | [11, 25] |
| $s_h$ | blsh | 1.3 | 0.4 | $\frac{1}{s}$ | Body lengths per second of hunting fish |  | [11, 32, 153] |
| $k_0$ | k3 | 16.6 | 0.498 | $\frac{g^{k_1}}{d}$ | For gut emptying, as in $k = k_0 {m_{PS}}^{-k_1}$ |  | [31] |
| $k_1$ | k1 | 0.28 | 0.025 | [ ] | For gut emptying, as in $k = k_0 {m_{PS}}^{-k_1}$ | Adjusted value = 0.2825 | [31] |
| $c_g$ | cg | 0.557 | 0.0557 | $\frac{cm^3}{g}$ | As in $V_g = c_g \cdot m_{PS}$ | Adjusted value = 0.520795 | [79][d] |
| $idiv$ | idiv | 12 | 1 | [ ] | Number of divisions for lengths in schools | Maximum number of schools | - |

[a] Value used for standard deviation in sensitivity analyses.
[b] For tilapia.
[c] At 20°$C$.
[d] For rainbow trout.
[e] For respiratory energy equivalent.

Table 2: Description and values of parameters related to reproduction.

| **Parameters related to reproduction** | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Variable Name** | | **Value** | **S.D.** | **Units** | **Description** | **Notes** | **Reference** |
| **In Text** | **In Code** | | | | | | |
| $e_{min}$ | emin | 0.0065 | 0.000559 | $\frac{g}{egg}$ | Minimum lipid per egg | | [35], [203][a] |
| $e_{max}$ | emax | 0.012 | 0.00103 | $\frac{g}{egg}$ | Maximum lipid per egg | | [35], [95][b] |
| $e_s$ | peg | 0.017 | 0.0015 | $\frac{g}{egg}$ | Structure per egg | | [35], [95][b] |
| $\eta$ | zlor | 16.3 | 1.63 | $cm$ | Length that must be reached for reproduction to occur | Intercept of egg production equation | [133] |
| $\sigma$ | smax | 124.2 | 12.42 | $\frac{eggs}{cm}$ | Slope of egg production equation | | [133] |
| | svary | 0.50 | 0.05 | [ ] | Fraction used to vary smax | | - |
| $A_1$ | a16 | 0.0003 | 0.00003 | $\frac{g}{egg}$ | Half-saturation constant modulated by $E_S$ | | Created |
| $A_2$ | a10 | 200.0 | 20.0 | $\frac{J}{g}$ | Energy to mobilize labile lipid for eggs | | Created |
| $A_3$ | a11 | 200.0 | 20.0 | $\frac{J}{g}$ | Energy to mobilize labile structure for eggs | | Created |
| Sept 1 | aa | 244 | 10 | $d$ | Start of time window for reproduction | Julian day 244 = September 1 | [65, 166] |
| Dec 31 | bb | 365 | 10 | $d$ | End of time window for reproduction | Julian day 365 = December 31 | [65, 166] |
| 3 | spwn1 | 3.0 | 1.0 | $^\circ C$ | Minimum lake temperature for spawning | | [166, 175] |
| 20 | spwn2 | 20.0 | 1.0 | $^\circ C$ | Maximum lake temperature for spawning | | [78, 166, 175] |
| | rmfec | 1500 | 500 | $eggs$ | Minimum fecundity when labile stores are large | | [62] |
| | resvar | 0.9999 | 0.0999 | [ ] | Fraction used to vary resource in egg calculation | | - |

[a] For onega salmon.
[b] For Atlantic salmon.

Table 3: Description and values of parameters related to migration.

| **Parameters related to migration** | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Variable Name** | | **Value** | **S.D.** | **Units** | **Description** | **Notes** | **Reference** |
| **In Text** | **In Code** | | | | | | |
| 1.55 | mmigl | 1.55 | 0.7 | $g$ | Minimum mass needed for lake to ocean migration to occur | Adjusted value = 1.48 | [28, 35, 100, 108] |
| First six months of the year | aal | 1 | 10 | $d$ | Start of time window for lake to ocean migration | Julian day 1 = January 1 | [35, 63, 92] |
| | bbl | 181 | 10 | $d$ | End of time window for lake to ocean migration | Julian day 181 = June 30 | [35, 63, 92] |
| 4 | migl1 | 4.0 | 0.5 | $°C$ | Minimum lake temperature for lake to ocean migration to occur | | [63, 78, 90, 92] |
| 17.5 | migl2 | 17.5 | 0.78 | $°C$ | Maximum lake temperature for lake to ocean migration to occur | | [63, 78, 92] |
| 600 | mmigo | 600.0 | 60.0 | $g$ | Minimum mass needed for ocean to lake migration to occur | | [88] |
| mid-June | aao | 172 | 10 | $d$ | Start of time window for ocean to lake migration | Julian day 172 = June 21 | [28] |
| mid-Sept | bbo | 263 | 10 | $d$ | End of time window for ocean to lake migration | Julian day 263 = September 20 | [28] |
| 110 | dist1 | 110.0 | 11.0 | $km$ | Distance from lake to coastal feeding grounds/river mouth | | [61, 76] |
| 2200 | dist2 | 3000.0 | 300.0 | $km$ | Distance from ocean to where feeding stops/river entrance | | [78] |
| $\zeta_1$ | trav1 | 15.0 | 5.0 | $\frac{km}{d}$ | Rate of travel during lake to ocean migration | | [28, 35] |
| $\zeta_2$ | trav2 | 50.0 | 10.0 | $\frac{km}{d}$ | Rate of travel during ocean to river entrance migration | | [21, 28, 78, 153] |
| $\zeta_3$ | trav3 | 5.6 | 0.8 | $\frac{km}{d}$ | Rate of travel during river entrance to lake migration | | [21] |
| $\psi_1$ | cost1 | 25.0 | 9.1 | $\frac{J/g}{km}$ | Migration cost per unit distance during lake to ocean migration | Using cost2 value | [28][a]; [75] |
| $\psi_2$, $\psi_3$ | cost2 | 25.0 | 9.1 | $\frac{J/g}{km}$ | Migration cost per unit distance during ocean to lake migration | | [28][a]; [75] |

[a] For wet weight to dry weight conversion.

Table 4: Description and values of parameters related to temperature modification.

| **Parameters related to temperature modification** | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Variable Name** | | **Value** | **S.D.** | **Units** | **Description** | **Notes** | **Reference** |
| **In Text** | **In Code** | | | | | | |
| $k_{opt1}$ | ehopt | 47.39 | | $d$ | Coefficient for hatching function | | [142] |
| $\alpha_1$ | ehalpha | 0.379 | | $\frac{1}{°C}$ | Exponent for hatching function | | [142] |
| $T_{opt1}$ | etopt | 14.0 | | $°C$ | Optimal temperature for hatching function | | [142] |
| $T_{max1}$ | ethigh | 25.0 | | $°C$ | Maximum temperature for hatching function | | [24, 25] |
| $k_{opt2}$ | fkopt | 0.99 | | [ ] | Coefficient for feeding function | | [98] |
| $\alpha_2$ | falpha | 0.075 | | $\frac{1}{°C}$ | Exponent for feeding function | | [98] |
| $T_{opt2}$ | ftopt | 17.0 | | $°C$ | Optimal temperature for feeding | | [26] |
| $T_{max2}$ | fthigh | 24.0 | | $°C$ | Highest temperature at which feeding can occur | | [26] |
| $\alpha_3$ | fk3a | 18.5 | | $°C$ | First coefficient for effect of temperature on k3 | | [31] |
| $\beta_3$ | fk3b | 0.0828 | | [ ] | Second coefficient for effect of temperature on k3 | | [31] |
| $\alpha_4$ | coefa | 0.31 | | [ ] | Coefficient for respiration function | | [27] |
| $\beta_4$ | coefb | 0.079 | | $\frac{1}{°C}$ | Exponent for respiration function | | [27] |
| $\alpha_5$ | fsdaa | 0.05353 | | [ ] | First coefficient for effect of temperature on apparent heat increment | | [12][a] |
| $\beta_5$ | fsdab | 0.063 | | $\frac{1}{°C}$ | Second coefficient for effect of temperature on apparent heat increment | | [12][a] |
| $\alpha_6$ | ema | 0.0148 | | $\frac{1}{°C^2}$ | Coefficient for egg mortality function | | [142] |
| $\beta_6$ | emb | 0.211 | | $\frac{1}{°C}$ | Second coefficient for egg mortality function | | [142] |
| $\gamma_6$ | emc | 0.0472 | | [ ] | Constant for egg mortality function | | [142] |
| $T_{low}$ | stlol | 1.0 | | $°C$ | Low temperature used for seasonal effects in the lake | | [28] |
| $T_{high}$ | sthil | 14.0 | | $°C$ | High temperature used for seasonal effects in the lake | | [26, 28] |
| $t_{peak}$ | peakl | 228 | | $d$ | Day when sthil occurs | Julian day 228 = August 15 | [26, 28] |
| $T_{low}$ | stloo | 4.5 | | $°C$ | Low temperature used for seasonal effects in the ocean | | [28] |
| $T_{high}$ | sthio | 12.0 | | $°C$ | High temperature used for seasonal effects in the ocean | | [28] |
| $t_{peak}$ | peako | 228 | | $d$ | Day when sthil occurs | Julian day 228 = August 15 | [26, 28] |

[a] For rainbow trout.

Table 5: Description and values of parameters related to resource.

| **Parameters related to resource (lake)** | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Variable Name** | | **Value** | **S.D.** | **Units** | **Description** | **Notes** | **Reference** |
| **In Text** | **In Code** | | | | | | |
| $\beta_p$ | betap | 0.003 | 0.002 | $\frac{g}{cm^3}$ | Allometric mass/length coefficient | | [76, 188] |
| $\frac{x_L}{x}$ | plx | 0.16 | 0.018 | [ ] | Fraction of lipid in lake resource | | [188] |
| $\frac{x_S}{x}$ | ppx | 0.72 | 0.021 | [ ] | Fraction of structure in resource | | [188] |
| $M_p$ | mp | 0.0000035 | 0.0000012 | $g$ | Mass of prey | | [56, 194] |
| $s_p$ | blsp | 1.6 | 0.25 | $\frac{1}{s}$ | Body lengths per second of escaping prey | | [71, 76] |
| $\rho_p$ | bdensp | 0.025 | 0.0025 | $\frac{g}{cm^3}$ | Body density of prey | | [76] |
| $a$ | alp | 30.0 | 1.5 | $cm^{-0.5}$ | As in reaction distance, $s_d = aL_p\sqrt{L_f}$ | | [22], [193][a] |
| **Parameters related to resource (ocean)** | | | | | | | |
| $x$ | resocean | 0.000003 | 0.000001 | $\frac{g}{cm^3}$ | Resource density in the ocean | | [94] |
| $\beta_p$ | obetap | 0.0012 | 0.0001 | $\frac{g}{cm^3}$ | Allometric mass/length coefficient | | [94, 147] |
| $\frac{x_S}{x}$ | oppx | 0.691 | 0.069 | [ ] | Fraction of structure in resource | Adjusted value = 0.66035 | [94] |
| $M_p$ | omp | 0.006375 | 0.00625 | $g$ | Mass of prey | | [94, 147] |
| $s_p$ | oblsp | 2.0 | 0.2 | $\frac{1}{s}$ | Body lengths per second of escaping prey | | Created |
| $\rho_p$ | obdensp | 0.025 | 0.0025 | $\frac{g}{cm^3}$ | Body density of prey | Adjusted value = 0.022625 | Created |
| $a$ | oalp | 30.0 | 1.5 | $cm^{-0.5}$ | As in reaction distance, $s_d = aL_p\sqrt{L_f}$ | | [22], [193][a] |

[a] For rainbow trout.

Table 6: Description and values of parameters related to mortality.

| Parameters related to mortality | | | | | | | |
|---|---|---|---|---|---|---|---|
| Variable Name | | Value | S.D. | Units | Description | Notes | Reference |
| In Text | In Code | | | | | | |
| $a_{max}$ | agemax | 2920.0 | | $d$ | Maximum age allowed | 2920 days = 8 years | - |
| $\nu_a$ | zmua | 0.1 | 0.01 | $\frac{1}{d}$ | Death coefficient for age | | Created |
| $\nu_{1a}$ | zmua1 | 0.00000025 | 0.000000025 | $\frac{1}{d}$ | Exponential coefficient for age in $\mu$ | | Created |
| $\nu_w$ | zmuw | 0.05 | 0.005 | $\frac{1}{g}$ | Death coefficient for biomass | Adjusted value = 0.04 | Created |
| $w_1$ | zmuw1 | 1.0 | 0.1 | $g$ | End of first individual biomass interval | | Created |
| $w_2$ | zmuw2 | 10.0 | 1.0 | $g$ | End of second individual biomass interval | | Created |
| $w_3$ | zmuw3 | 160.0 | 16.0 | $g$ | End of third individual biomass interval | | Created |
| $v_0$ | zmuv0 | 0.5 | 0.05 | $\frac{1}{d}$ | Initial value of individual biomass death coefficient | Adjusted value = 0.4 | Created |
| $v_c$ | zmuvc | 0.001 | 0.0001 | $\frac{1}{d}$ | Constant value of individual biomass death coefficient | | Created |
| $v_f$ | zmuvf | 0.1 | 0.01 | $\frac{1}{d}$ | Final value of individual biomass death coefficient | Adjusted value = 0.08 | Created |
| $p_t$ | thresh | 5000.0 | 500.0 | $g$ | Threshold value for biomass in lake | | Created |
| $p_t$ | thresho | 50000.0 | 5000.0 | $g$ | Threshold value for biomass in ocean | | Created |
| $p_o$ | bopt | 50000.0 | 5000.0 | $g$ | Optimal value for biomass in lake | | Created |
| $p_o$ | bopto | 500000.0 | 50000.0 | $g$ | Optimal value for biomass in ocean | | Created |
| $p_c$ | zcap | 500000.0 | 50000.0 | $g$ | Biomass carrying capacity in lake | | Created |
| $p_c$ | zcapo | 5000000.0 | 500000.0 | $g$ | Biomass carrying capacity in ocean | | Created |
| $d_m$ | zmudm | 0.002 | 0.0002 | $\frac{1}{d}$ | Maximum density death value in lake | | Created |
| $d_m$ | zmudmo | 0.0002 | 0.00002 | $\frac{1}{d}$ | Maximum density death value in ocean | | Created |
| $a_{yoymin}$ | yoymin | 18.0 | 1.0 | $d$ | Minimum young-of-year age | | Created |
| $a_{yoymax}$ | yoymax | 60.0 | 1.0 | $d$ | Maximum young-of-year age | | Created |
| $p_{yoy_o}$ | yoyopt | 8000.0 | 800.0 | # | Optimal number for young-of-year | Adjusted value = 0.08 | Created |
| $p_{yoy_c}$ | yoycap | 10000.0 | 1000.0 | # | Capacity for number of young-of-year | | Created |
| $y_m$ | yoymort | 0.1 | 0.01 | $\frac{1}{d}$ | Maximum mortality for young-of-year | | Created |
| $c_{sch}$ | fdensrc | 100.0 | 10.0 | $\frac{\#}{V}$ | Constant in fdensr subroutine function | | Created |
| $d_{sch}$ | fdensmuc | 100.0 | 10.0 | $\frac{\#}{V}$ | Constant in fdensmu subroutine | | Created |

Table 7: Life history stages.

| **Life Stage** | | **Feeding?** | **Schooling?** | **Temperature Function** | **Resource** | **Loss Terms** |
|---|---|---|---|---|---|---|
| Lake | Yolk-sac | No | No | Lake | N/A | Maintenance |
| | Post yolk-sac | Yes | Yes | Lake | *Cyclops* | Maintenance + Apparent heat increment + Work associated with pursuit and capture of prey items |
| Migration from lake to coast/ocean | | No | Yes | Lake | N/A | Maintenance + Work associated with migration |
| Ocean | | Yes | No | Ocean | *Thysanoessa* | Maintenance + Apparent heat increment + Work associated with pursuit and capture of prey items |
| Migration from ocean to river entrance | | Yes | No | Ocean | *Thysanoessa* | Maintenance + Apparent heat increment + Work associated with pursuit and capture of prey items + Work associated with migration |
| Migration from river entrance to lake | | No | No | Lake | N/A | Maintenance + Work associate with migration |
| Lake (Adult) | | No | No | Lake | N/A | Maintenance + Reproduction |

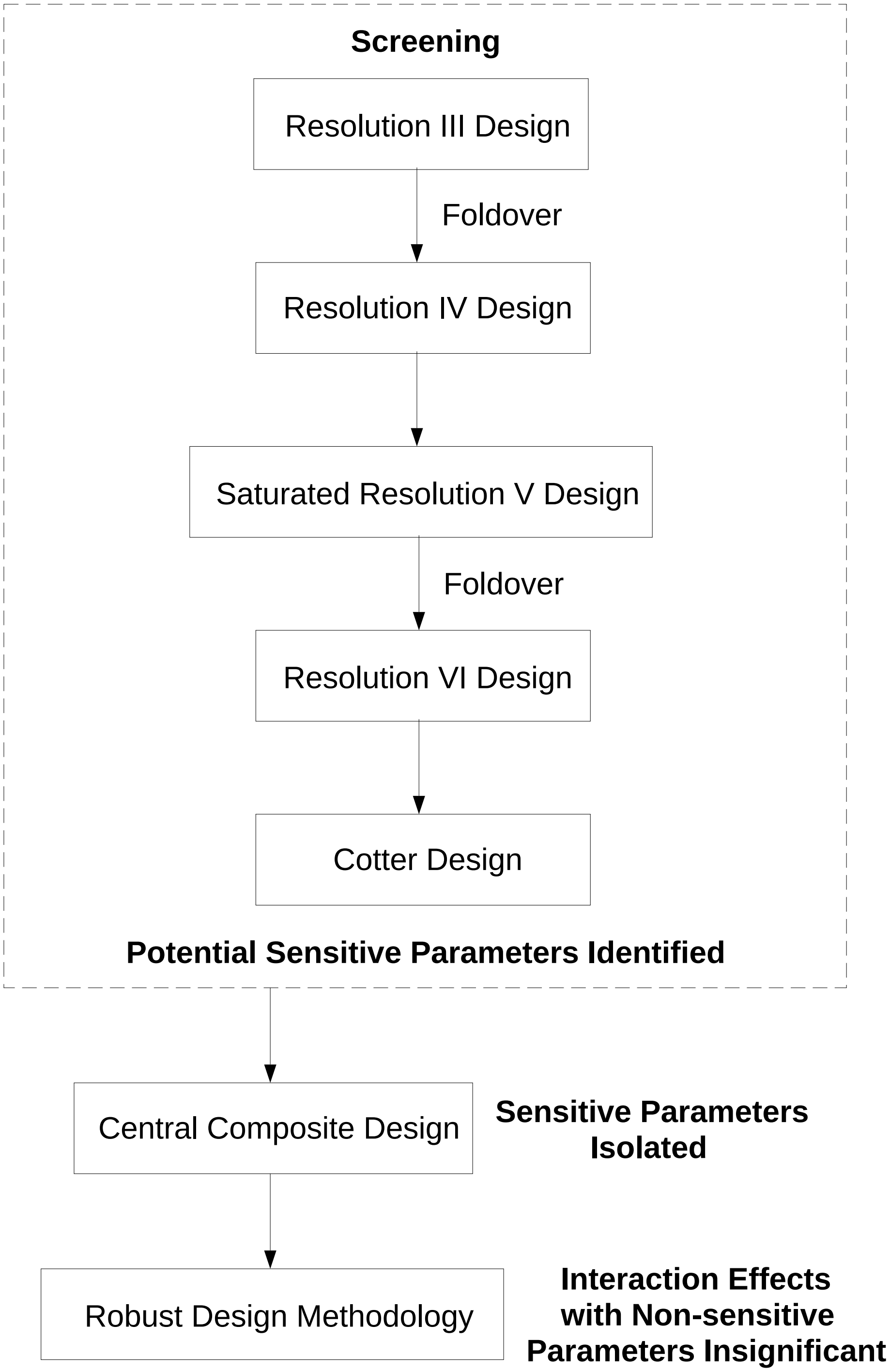

Figure 2: Sequential experimentation implemented for the sensitivity analysis of the individual model.

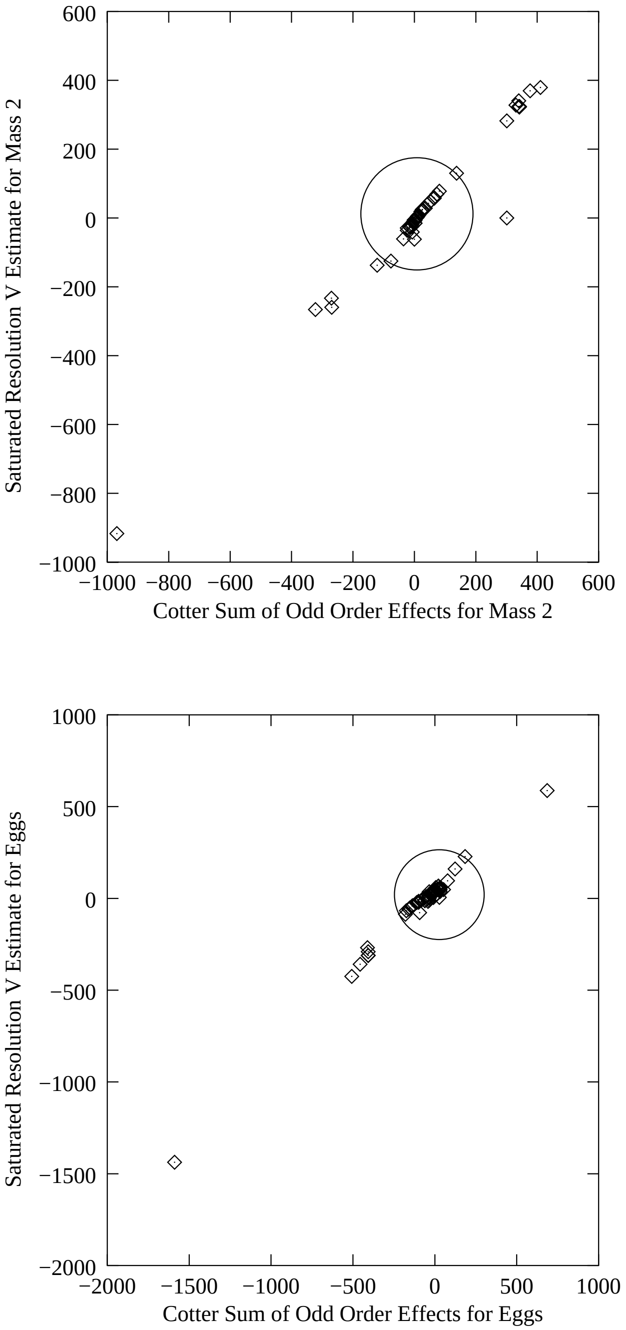

Figure 3: Saturated resolution $V$ estimates plotted against the sums of the odd Cotter estimates for $Mass$ 2 and $Eggs$.

Table 8: Parameters to which the outputs, $Mass$ 2, $Mass$ 3, and $Eggs$, were found to be sensitive. Parameters are listed from most to least influence.

| **Mass 2** | | **Mass 3** | | **Eggs** | |
|---|---|---|---|---|---|
| Highly Sensitive | Slightly Sensitive | Highly Sensitive | Slightly Sensitive | Highly Sensitive | Slightly Sensitive |
| $k1$ | $templ$ | $k1$ | $templ$ | $templ$ | $zjmgp$ |
| $tempo$ | $a0l$ | $a6$ | $a0l$ | $oppx$ | $resvar$ |
| $oppx$ | $zjmgp$ | $oppx$ | $oplx$ | $a6$ | $oplx$ |
| $a0p$ | $bdensp$ | $tempo$ | $zjmgp$ | $cg$ | $a3$ |
| $a6$ | $a4$ | $a0p$ | $bdensp$ | $obdensp$ | $a4$ |
| $obdensp$ | $a3$ | $obdensp$ | $a4$ | $a0p$ | $a0l$ |
| $cg$ | $oplx$ | $cg$ | $a3$ | $tempo$ | |
| | $zjmgl$ | | $zjmgl$ | $k1$ | |
| | $blsp$ | | $blsp$ | | |

Table 9: Ecotypes which compose the population.

| **oplx** | **a01** | **a3** | **a4** | **Resource Level** | **Assigned Number** |
|---|---|---|---|---|---|
| 0.173 | 0.85 | 0.12 | 0.37 | Middle | 1 |
| 0.173 | 0.85 | 0.12 | 0.40367 | Middle | 2 |
| 0.173 | 0.85 | 0.12 | 0.43734 | Middle | 3 |
| 0.173 | 0.85 | 0.10908 | 0.37 | Middle | 4 |
| 0.173 | 0.85 | 0.10908 | 0.40367 | Middle | 5 |
| 0.173 | 0.85 | 0.10908 | 0.43734 | Middle | 6 |
| 0.173 | 0.85 | 0.09816 | 0.37 | Middle | 7 |
| 0.173 | 0.85 | 0.09816 | 0.40367 | Middle | 8 |
| 0.173 | 0.85 | 0.09816 | 0.43734 | Middle | 9 |
| 0.173 | 0.8045 | 0.12 | 0.37 | Middle | 10 |
| 0.173 | 0.8045 | 0.12 | 0.40367 | Middle | 11 |
| 0.173 | 0.8045 | 0.12 | 0.43734 | Middle | 12 |
| 0.173 | 0.8045 | 0.10908 | 0.37 | Middle | 13 |
| 0.173 | 0.8045 | 0.10908 | 0.40367 | Middle | 14 |
| 0.173 | 0.8045 | 0.10908 | 0.43734 | Middle | 15 |
| 0.173 | 0.8045 | 0.09816 | 0.37 | Middle | 16 |
| 0.173 | 0.8045 | 0.09816 | 0.40367 | Middle | 17 |
| 0.173 | 0.8045 | 0.09816 | 0.43734 | Middle | 18 |
| 0.173 | 0.759 | 0.12 | 0.37 | Middle | 19 |
| 0.173 | 0.759 | 0.12 | 0.40367 | Middle | 20 |
| 0.173 | 0.759 | 0.12 | 0.43734 | Middle | 21 |
| 0.173 | 0.759 | 0.10908 | 0.37 | Middle | 22 |
| 0.173 | 0.759 | 0.10908 | 0.40367 | Middle | 23 |
| 0.173 | 0.759 | 0.10908 | 0.43734 | Middle | 24 |
| 0.173 | 0.759 | 0.09816 | 0.37 | Middle | 25 |
| 0.173 | 0.759 | 0.09816 | 0.40367 | Middle | 26 |
| 0.173 | 0.759 | 0.09816 | 0.43734 | Middle | 27 |
| 0.157257 | 0.85 | 0.12 | 0.37 | Middle | 28 |
| 0.157257 | 0.85 | 0.12 | 0.40367 | Middle | 29 |
| 0.157257 | 0.85 | 0.12 | 0.43734 | Middle | 30 |
| 0.157257 | 0.85 | 0.10908 | 0.37 | Middle | 31 |
| 0.157257 | 0.85 | 0.10908 | 0.40367 | Middle | 32 |
| 0.157257 | 0.85 | 0.10908 | 0.43734 | Middle | 33 |
| 0.157257 | 0.85 | 0.09816 | 0.37 | Middle | 34 |
| 0.157257 | 0.85 | 0.09816 | 0.40367 | Middle | 35 |
| 0.157257 | 0.85 | 0.09816 | 0.43734 | Middle | 36 |
| 0.157257 | 0.8045 | 0.12 | 0.37 | Middle | 37 |
| 0.157257 | 0.8045 | 0.12 | 0.40367 | Middle | 38 |
| 0.157257 | 0.8045 | 0.12 | 0.43734 | Middle | 39 |
| 0.157257 | 0.8045 | 0.10908 | 0.37 | Middle | 40 |
| 0.157257 | 0.8045 | 0.10908 | 0.40367 | Middle | 41 |
| 0.157257 | 0.8045 | 0.10908 | 0.43734 | Middle | 42 |
| 0.157257 | 0.8045 | 0.09816 | 0.37 | Middle | 43 |
| 0.157257 | 0.8045 | 0.09816 | 0.40367 | Middle | 44 |
| 0.157257 | 0.8045 | 0.09816 | 0.43734 | Middle | 45 |
| 0.157257 | 0.759 | 0.12 | 0.37 | Middle | 46 |
| 0.157257 | 0.759 | 0.12 | 0.40367 | Middle | 47 |
| 0.157257 | 0.759 | 0.12 | 0.43734 | Middle | 48 |
| 0.157257 | 0.759 | 0.10908 | 0.37 | Middle | 49 |
| 0.157257 | 0.759 | 0.10908 | 0.40367 | Middle | 50 |

Table 9 (continued).

| **oplx** | **a01** | **a3** | **a4** | **Resource Level** | **Assigned Number** |
|---|---|---|---|---|---|
| 0.157257 | 0.759 | 0.10908 | 0.43734 | Middle | 51 |
| 0.157257 | 0.759 | 0.09816 | 0.37 | Middle | 52 |
| 0.157257 | 0.759 | 0.09816 | 0.40367 | Middle | 53 |
| 0.157257 | 0.759 | 0.09816 | 0.43734 | Middle | 54 |
| 0.141514 | 0.85 | 0.12 | 0.37 | Middle | 55 |
| 0.141514 | 0.85 | 0.12 | 0.40367 | Middle | 56 |
| 0.141514 | 0.85 | 0.12 | 0.43734 | Middle | 57 |
| 0.141514 | 0.85 | 0.10908 | 0.37 | Middle | 58 |
| 0.141514 | 0.85 | 0.10908 | 0.40367 | Middle | 59 |
| 0.141514 | 0.85 | 0.10908 | 0.43734 | Middle | 60 |
| 0.141514 | 0.85 | 0.09816 | 0.37 | Middle | 61 |
| 0.141514 | 0.85 | 0.09816 | 0.40367 | Middle | 62 |
| 0.141514 | 0.85 | 0.09816 | 0.43734 | Middle | 63 |
| 0.141514 | 0.8045 | 0.12 | 0.37 | Middle | 64 |
| 0.141514 | 0.8045 | 0.12 | 0.40367 | Middle | 65 |
| 0.141514 | 0.8045 | 0.12 | 0.43734 | Middle | 66 |
| 0.141514 | 0.8045 | 0.10908 | 0.37 | Middle | 67 |
| 0.141514 | 0.8045 | 0.10908 | 0.40367 | Middle | 68 |
| 0.141514 | 0.8045 | 0.10908 | 0.43734 | Middle | 69 |
| 0.141514 | 0.8045 | 0.09816 | 0.37 | Middle | 70 |
| 0.141514 | 0.8045 | 0.09816 | 0.40367 | Middle | 71 |
| 0.141514 | 0.8045 | 0.09816 | 0.43734 | Middle | 72 |
| 0.141514 | 0.759 | 0.12 | 0.37 | Middle | 73 |
| 0.141514 | 0.759 | 0.12 | 0.40367 | Middle | 74 |
| 0.141514 | 0.759 | 0.12 | 0.43734 | Middle | 75 |
| 0.141514 | 0.759 | 0.10908 | 0.37 | Middle | 76 |
| 0.141514 | 0.759 | 0.10908 | 0.40367 | Middle | 77 |
| 0.141514 | 0.759 | 0.10908 | 0.43734 | Middle | 78 |
| 0.141514 | 0.759 | 0.09816 | 0.37 | Middle | 79 |
| 0.141514 | 0.759 | 0.09816 | 0.40367 | Middle | 80 |
| 0.141514 | 0.759 | 0.09816 | 0.43734 | Middle | 81 |
| 0.173 | 0.85 | 0.12 | 0.37 | Low | 82 |
| 0.173 | 0.85 | 0.12 | 0.40367 | Low | 83 |
| 0.173 | 0.85 | 0.12 | 0.43734 | Low | 84 |
| 0.173 | 0.85 | 0.10908 | 0.37 | Low | 85 |
| 0.173 | 0.85 | 0.10908 | 0.40367 | Low | 86 |
| 0.173 | 0.85 | 0.10908 | 0.43734 | Low | 87 |
| 0.173 | 0.85 | 0.09816 | 0.37 | Low | 88 |
| 0.173 | 0.85 | 0.09816 | 0.40367 | Low | 89 |
| 0.173 | 0.85 | 0.09816 | 0.43734 | Low | 90 |
| 0.173 | 0.8045 | 0.12 | 0.37 | Low | 91 |
| 0.173 | 0.8045 | 0.12 | 0.40367 | Low | 92 |
| 0.173 | 0.8045 | 0.12 | 0.43734 | Low | 93 |
| 0.173 | 0.8045 | 0.10908 | 0.37 | Low | 94 |
| 0.173 | 0.8045 | 0.10908 | 0.40367 | Low | 95 |
| 0.173 | 0.8045 | 0.10908 | 0.43734 | Low | 96 |
| 0.173 | 0.8045 | 0.09816 | 0.37 | Low | 97 |
| 0.173 | 0.8045 | 0.09816 | 0.40367 | Low | 98 |
| 0.173 | 0.8045 | 0.09816 | 0.43734 | Low | 99 |
| 0.173 | 0.759 | 0.12 | 0.37 | Low | 100 |

Table 9 (continued).

| **oplx** | **a01** | **a3** | **a4** | **Resource Level** | **Assigned Number** |
|---|---|---|---|---|---|
| 0.173 | 0.759 | 0.12 | 0.40367 | Low | 101 |
| 0.173 | 0.759 | 0.12 | 0.43734 | Low | 102 |
| 0.173 | 0.759 | 0.10908 | 0.37 | Low | 103 |
| 0.173 | 0.759 | 0.10908 | 0.40367 | Low | 104 |
| 0.173 | 0.759 | 0.10908 | 0.43734 | Low | 105 |
| 0.173 | 0.759 | 0.09816 | 0.37 | Low | 106 |
| 0.173 | 0.759 | 0.09816 | 0.40367 | Low | 107 |
| 0.173 | 0.759 | 0.09816 | 0.43734 | Low | 108 |
| 0.157257 | 0.85 | 0.12 | 0.37 | Low | 109 |
| 0.157257 | 0.85 | 0.12 | 0.40367 | Low | 110 |
| 0.157257 | 0.85 | 0.12 | 0.43734 | Low | 111 |
| 0.157257 | 0.85 | 0.10908 | 0.37 | Low | 112 |
| 0.157257 | 0.85 | 0.10908 | 0.40367 | Low | 113 |
| 0.157257 | 0.85 | 0.10908 | 0.43734 | Low | 114 |
| 0.157257 | 0.85 | 0.09816 | 0.37 | Low | 115 |
| 0.157257 | 0.85 | 0.09816 | 0.40367 | Low | 116 |
| 0.157257 | 0.85 | 0.09816 | 0.43734 | Low | 117 |
| 0.157257 | 0.8045 | 0.12 | 0.37 | Low | 118 |
| 0.157257 | 0.8045 | 0.12 | 0.40367 | Low | 119 |
| 0.157257 | 0.8045 | 0.12 | 0.43734 | Low | 120 |
| 0.157257 | 0.8045 | 0.10908 | 0.37 | Low | 121 |
| 0.157257 | 0.8045 | 0.10908 | 0.40367 | Low | 122 |
| 0.157257 | 0.8045 | 0.10908 | 0.43734 | Low | 123 |
| 0.157257 | 0.8045 | 0.09816 | 0.37 | Low | 124 |
| 0.157257 | 0.8045 | 0.09816 | 0.40367 | Low | 125 |
| 0.157257 | 0.8045 | 0.09816 | 0.43734 | Low | 126 |
| 0.157257 | 0.759 | 0.12 | 0.37 | Low | 127 |
| 0.157257 | 0.759 | 0.12 | 0.40367 | Low | 128 |
| 0.157257 | 0.759 | 0.12 | 0.43734 | Low | 129 |
| 0.157257 | 0.759 | 0.10908 | 0.37 | Low | 130 |
| 0.157257 | 0.759 | 0.10908 | 0.40367 | Low | 131 |
| 0.157257 | 0.759 | 0.10908 | 0.43734 | Low | 132 |
| 0.157257 | 0.759 | 0.09816 | 0.37 | Low | 133 |
| 0.157257 | 0.759 | 0.09816 | 0.40367 | Low | 134 |
| 0.157257 | 0.759 | 0.09816 | 0.43734 | Low | 135 |
| 0.141514 | 0.85 | 0.12 | 0.37 | Low | 136 |
| 0.141514 | 0.85 | 0.12 | 0.40367 | Low | 137 |
| 0.141514 | 0.85 | 0.12 | 0.43734 | Low | 138 |
| 0.141514 | 0.85 | 0.10908 | 0.37 | Low | 139 |
| 0.141514 | 0.85 | 0.10908 | 0.40367 | Low | 140 |
| 0.141514 | 0.85 | 0.10908 | 0.43734 | Low | 141 |
| 0.141514 | 0.85 | 0.09816 | 0.37 | Low | 142 |
| 0.141514 | 0.85 | 0.09816 | 0.40367 | Low | 143 |
| 0.141514 | 0.85 | 0.09816 | 0.43734 | Low | 144 |
| 0.141514 | 0.8045 | 0.12 | 0.37 | Low | 145 |
| 0.141514 | 0.8045 | 0.12 | 0.40367 | Low | 146 |
| 0.141514 | 0.8045 | 0.12 | 0.43734 | Low | 147 |
| 0.141514 | 0.8045 | 0.10908 | 0.37 | Low | 148 |
| 0.141514 | 0.8045 | 0.10908 | 0.40367 | Low | 149 |
| 0.141514 | 0.8045 | 0.10908 | 0.43734 | Low | 150 |

Table 9 (continued).

| **oplx** | **a01** | **a3** | **a4** | **Resource Level** | **Assigned Number** |
|---|---|---|---|---|---|
| 0.141514 | 0.8045 | 0.09816 | 0.37 | Low | 151 |
| 0.141514 | 0.8045 | 0.09816 | 0.40367 | Low | 152 |
| 0.141514 | 0.8045 | 0.09816 | 0.43734 | Low | 153 |
| 0.141514 | 0.759 | 0.12 | 0.37 | Low | 154 |
| 0.141514 | 0.759 | 0.12 | 0.40367 | Low | 155 |
| 0.141514 | 0.759 | 0.12 | 0.43734 | Low | 156 |
| 0.141514 | 0.759 | 0.10908 | 0.37 | Low | 157 |
| 0.141514 | 0.759 | 0.10908 | 0.40367 | Low | 158 |
| 0.141514 | 0.759 | 0.10908 | 0.43734 | Low | 159 |
| 0.141514 | 0.759 | 0.09816 | 0.37 | Low | 160 |
| 0.141514 | 0.759 | 0.09816 | 0.40367 | Low | 161 |
| 0.141514 | 0.759 | 0.09816 | 0.43734 | Low | 162 |
| 0.173 | 0.85 | 0.12 | 0.37 | High | 163 |
| 0.173 | 0.85 | 0.12 | 0.40367 | High | 164 |
| 0.173 | 0.85 | 0.12 | 0.43734 | High | 165 |
| 0.173 | 0.85 | 0.10908 | 0.37 | High | 166 |
| 0.173 | 0.85 | 0.10908 | 0.40367 | High | 167 |
| 0.173 | 0.85 | 0.10908 | 0.43734 | High | 168 |
| 0.173 | 0.85 | 0.09816 | 0.37 | High | 169 |
| 0.173 | 0.85 | 0.09816 | 0.40367 | High | 170 |
| 0.173 | 0.85 | 0.09816 | 0.43734 | High | 171 |
| 0.173 | 0.8045 | 0.12 | 0.37 | High | 172 |
| 0.173 | 0.8045 | 0.12 | 0.40367 | High | 173 |
| 0.173 | 0.8045 | 0.12 | 0.43734 | High | 174 |
| 0.173 | 0.8045 | 0.10908 | 0.37 | High | 175 |
| 0.173 | 0.8045 | 0.10908 | 0.40367 | High | 176 |
| 0.173 | 0.8045 | 0.10908 | 0.43734 | High | 177 |
| 0.173 | 0.8045 | 0.09816 | 0.37 | High | 178 |
| 0.173 | 0.8045 | 0.09816 | 0.40367 | High | 179 |
| 0.173 | 0.8045 | 0.09816 | 0.43734 | High | 180 |
| 0.173 | 0.759 | 0.12 | 0.37 | High | 181 |
| 0.173 | 0.759 | 0.12 | 0.40367 | High | 182 |
| 0.173 | 0.759 | 0.12 | 0.43734 | High | 183 |
| 0.173 | 0.759 | 0.10908 | 0.37 | High | 184 |
| 0.173 | 0.759 | 0.10908 | 0.40367 | High | 185 |
| 0.173 | 0.759 | 0.10908 | 0.43734 | High | 186 |
| 0.173 | 0.759 | 0.09816 | 0.37 | High | 187 |
| 0.173 | 0.759 | 0.09816 | 0.40367 | High | 188 |
| 0.173 | 0.759 | 0.09816 | 0.43734 | High | 189 |
| 0.157257 | 0.85 | 0.12 | 0.37 | High | 190 |
| 0.157257 | 0.85 | 0.12 | 0.40367 | High | 191 |
| 0.157257 | 0.85 | 0.12 | 0.43734 | High | 192 |
| 0.157257 | 0.85 | 0.10908 | 0.37 | High | 193 |
| 0.157257 | 0.85 | 0.10908 | 0.40367 | High | 194 |
| 0.157257 | 0.85 | 0.10908 | 0.43734 | High | 195 |
| 0.157257 | 0.85 | 0.09816 | 0.37 | High | 196 |
| 0.157257 | 0.85 | 0.09816 | 0.40367 | High | 197 |
| 0.157257 | 0.85 | 0.09816 | 0.43734 | High | 198 |
| 0.157257 | 0.8045 | 0.12 | 0.37 | High | 199 |
| 0.157257 | 0.8045 | 0.12 | 0.40367 | High | 200 |

Table 9 (continued).

| **oplx** | **a01** | **a3** | **a4** | **Resource Level** | **Assigned Number** |
|---|---|---|---|---|---|
| 0.157257 | 0.8045 | 0.12 | 0.43734 | High | 201 |
| 0.157257 | 0.8045 | 0.10908 | 0.37 | High | 202 |
| 0.157257 | 0.8045 | 0.10908 | 0.40367 | High | 203 |
| 0.157257 | 0.8045 | 0.10908 | 0.43734 | High | 204 |
| 0.157257 | 0.8045 | 0.09816 | 0.37 | High | 205 |
| 0.157257 | 0.8045 | 0.09816 | 0.40367 | High | 206 |
| 0.157257 | 0.8045 | 0.09816 | 0.43734 | High | 207 |
| 0.157257 | 0.759 | 0.12 | 0.37 | High | 208 |
| 0.157257 | 0.759 | 0.12 | 0.40367 | High | 209 |
| 0.157257 | 0.759 | 0.12 | 0.43734 | High | 210 |
| 0.157257 | 0.759 | 0.10908 | 0.37 | High | 211 |
| 0.157257 | 0.759 | 0.10908 | 0.40367 | High | 212 |
| 0.157257 | 0.759 | 0.10908 | 0.43734 | High | 213 |
| 0.157257 | 0.759 | 0.09816 | 0.37 | High | 214 |
| 0.157257 | 0.759 | 0.09816 | 0.40367 | High | 215 |
| 0.157257 | 0.759 | 0.09816 | 0.43734 | High | 216 |
| 0.141514 | 0.85 | 0.12 | 0.37 | High | 217 |
| 0.141514 | 0.85 | 0.12 | 0.40367 | High | 218 |
| 0.141514 | 0.85 | 0.12 | 0.43734 | High | 219 |
| 0.141514 | 0.85 | 0.10908 | 0.37 | High | 220 |
| 0.141514 | 0.85 | 0.10908 | 0.40367 | High | 221 |
| 0.141514 | 0.85 | 0.10908 | 0.43734 | High | 222 |
| 0.141514 | 0.85 | 0.09816 | 0.37 | High | 223 |
| 0.141514 | 0.85 | 0.09816 | 0.40367 | High | 224 |
| 0.141514 | 0.85 | 0.09816 | 0.43734 | High | 225 |
| 0.141514 | 0.8045 | 0.12 | 0.37 | High | 226 |
| 0.141514 | 0.8045 | 0.12 | 0.40367 | High | 227 |
| 0.141514 | 0.8045 | 0.12 | 0.43734 | High | 228 |
| 0.141514 | 0.8045 | 0.10908 | 0.37 | High | 229 |
| 0.141514 | 0.8045 | 0.10908 | 0.40367 | High | 230 |
| 0.141514 | 0.8045 | 0.10908 | 0.43734 | High | 231 |
| 0.141514 | 0.8045 | 0.09816 | 0.37 | High | 232 |
| 0.141514 | 0.8045 | 0.09816 | 0.40367 | High | 233 |
| 0.141514 | 0.8045 | 0.09816 | 0.43734 | High | 234 |
| 0.141514 | 0.759 | 0.12 | 0.37 | High | 235 |
| 0.141514 | 0.759 | 0.12 | 0.40367 | High | 236 |
| 0.141514 | 0.759 | 0.12 | 0.43734 | High | 237 |
| 0.141514 | 0.759 | 0.10908 | 0.37 | High | 238 |
| 0.141514 | 0.759 | 0.10908 | 0.40367 | High | 239 |
| 0.141514 | 0.759 | 0.10908 | 0.43734 | High | 240 |
| 0.141514 | 0.759 | 0.09816 | 0.37 | High | 241 |
| 0.141514 | 0.759 | 0.09816 | 0.40367 | High | 242 |
| 0.141514 | 0.759 | 0.09816 | 0.43734 | High | 243 |

Table 10: Ecotypes surviving under different resource and schooling conditions.

| **Maximum Possible Number of Schools** | **Resource Level** [g/cm$^3$ · $10^{-6}$] | | |
|---|---|---|---|
| | **Low = 0.03**<br>**Middle = 0.06**<br>**High = 0.09** | **Low = 0.06**<br>**Middle = 0.12**<br>**High = 0.18** | **Low = 0.12**<br>**Middle = 0.18**<br>**High = 0.24** |
| 1 | 0 | 28, 109, 190 | 55, 78, 136, 159, 217, 240[a] |
| 2 | 72, 88 | 34, 159[a] | 34, 81 |
| 3 | 28, 81, 238 | 190, 242, 243 | 81 |
| 4 | 79, 243 | 1, 235, 241, 243 | 1, 155, 163, 242 |
| 5 | 80, 162 | 78, 81 | 80, 144, 163 |
| 6 | 162 | 7, 80 | 162 |
| 7 | 64, 238 | 73 | 162, 242 |
| 8 | 78, 80, 153 | 220, 224 | 80, 149 |
| 9 | 80, 81 | 1, 73, 82, 240 | 162, 241 |
| 10 | 83, 129, 217 | 27, 160 | 1, 163, 241, 242 |
| 11 | 156, 235 | 223 | 1, 144, 163 |
| 12 | 134, 141, 162 | 167, 242 | 1, 145, 163, 242 |

[a] Simulation had not reached steady state after 10000 years.

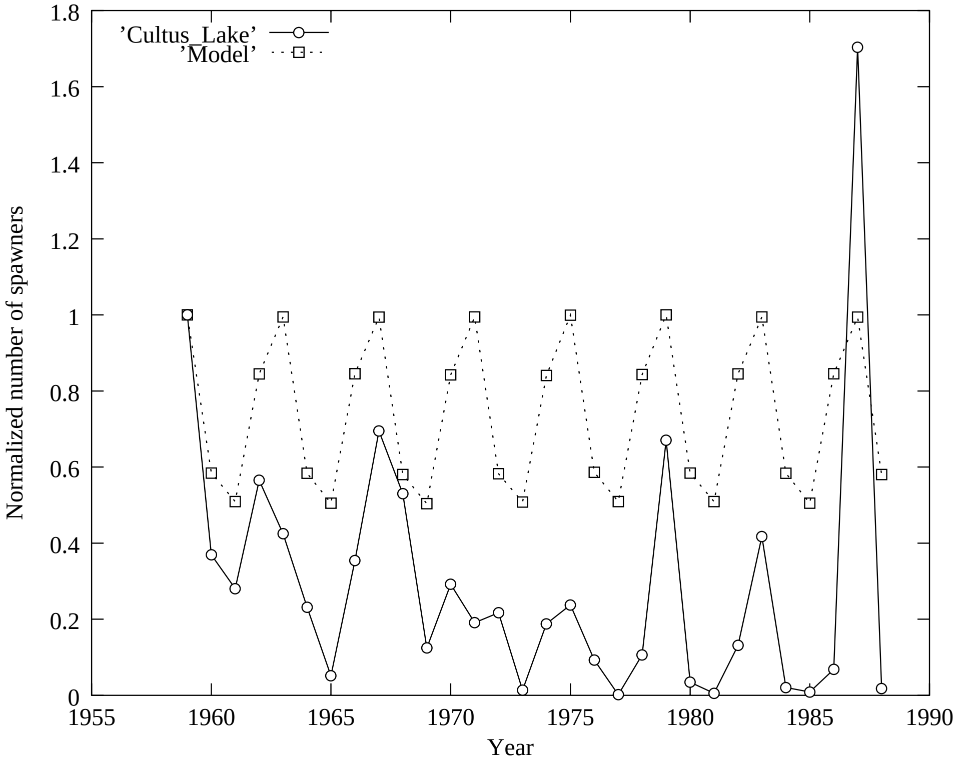

Figure 4: Model/data comparison for returning number of spawners at Cultus Lake.

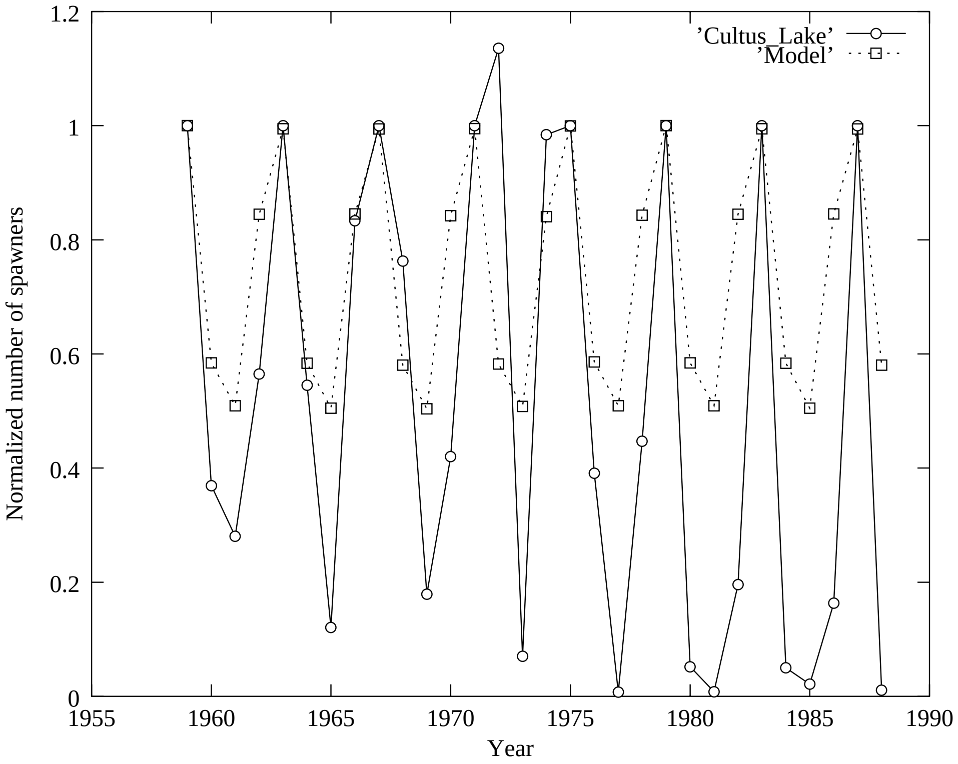

Figure 5: Model/data comparison for returning number of spawners at Cultus Lake using adaptive fitting.

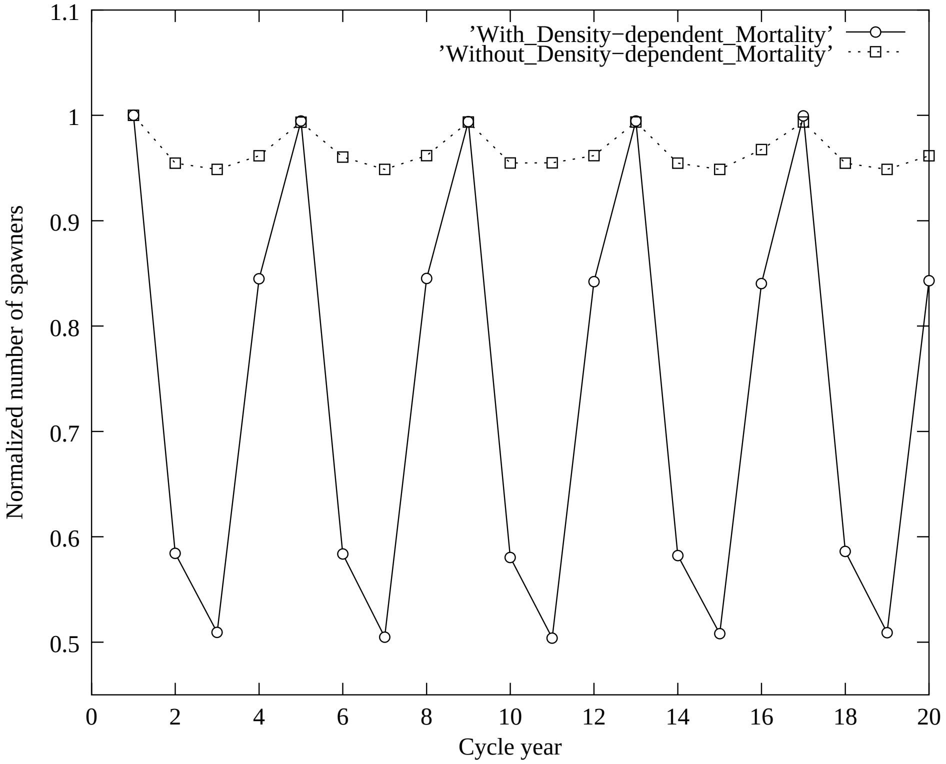

Figure 6: Cycles occurring with and without density-dependent mortality.

# Appendix II

The amount of time that it takes for the yolk-sac to be absorbed and external feeding to begin is given by $f_1(T)$ $[d]$. Following the representation developed by Lassiter (1975) describing the effect of temperature on the biological response of an individual organism, $f_1(T)$ is given by

$$k_{opt_1} e^{\alpha_1 (T - T_{opt_1})} \left( \frac{T_{max_1} - T}{T_{max_1} - T_{opt_1}} \right)^{\alpha_1 (T_{max_1} - T_{opt_1})} \tag{II.1}$$

where $k_{opt_1}$ is the optimal value for $f_1$ evaluated at the temperature, $T_{opt_1}$ $[^\circ C]$, which results in the smallest number of days for the length of the embryonic stage, and $T_{max_1}$ $[^\circ C]$ is the upper lethal temperature for sockeye. The parameters $k_{opt_1}$ and $\alpha_1$ are both fitted using values from [142].

The function of temperature which modifies the feeding rate is given by $f_2(T)$ $[\ ]$. Again, following the representation developed by [123], $f_2(T)$ is represented by

$$k_{opt_2} e^{\alpha_2 (T - T_{opt_2})} \left( \frac{T_{max_2} - T}{T_{max_2} - T_{opt_2}} \right)^{\alpha_2 (T_{max_2} - T_{opt_2})} \tag{II.2}$$

where $k_{opt_2}$ is the optimal value for $f_2$ evaluated at the optimal temperature for feeding, $T_{opt_2}$ $[^\circ C]$, and $T_{max_2}$ $[^\circ C]$ is the minimum temperature above $T_{opt_2}$ at which feeding ceases to occur. $k_{opt_2}$ and $\alpha_2$ are both fitted parameters using values from Hewett and Johnson's (1992) model parameterized for sockeye salmon. $f_2(T)$ is set up to give values between 0 and 1; when equation (II.2) becomes negative, a value of 0 is assumed.

The gut clearance rate is modified by a function of temperature, $f_3(T)$ [ ], which is given by

$$f_3(T) = \begin{cases} \frac{T}{\alpha_3 - \beta_3 T} & \text{for } T \geq 0°C \\ 0 & \text{otherwise} \end{cases} \tag{II.3}$$

The parameters, $\alpha_3$ and $\beta_3$, are fitted using sockeye salmon data from [31] which accounts for both size and temperature.

The maintenance requirements of an individual are modified by the temperature function, $f_4(T)$ [ ]. The function $f_4(T)$ has an exponential relationship represented by $\alpha_4 e^{\beta_4 T}$ where $\alpha_4$ and $\beta_4$ are fitted parameters using data from [27].

The value for apparent heat increment given as a function of temperature is $f_5(T) = \alpha_5 e^{\beta_5 T}$ where $\alpha_5$ and $\beta_5$ are fitted parameters. The same apparent heat increment value is used for both lipids and protein.

The fraction of eggs that survive given as a function of temperature is

$$f_6(T) = \begin{cases} -\alpha_6 T^2 + \beta_6 T + \gamma_6 & \text{for } \frac{\beta_6 - \sqrt{\beta_6{}^2 + 4\alpha_6\gamma_6}}{2\alpha_6} \leq T \leq \frac{\beta_6 + \sqrt{\beta_6{}^2 + 4\alpha_6\gamma_6}}{2\alpha_6} \\ 0 & \text{otherwise} \end{cases} \tag{II.4}$$

where $\alpha_6$, $\beta_6$, and $\gamma_6$ are fitted parameters using sockeye salmon data from [142] and rescaling to give 79% survival at a temperature of $8°C$. Note that 100% survival of eggs is not allowed because there are always nonviable eggs in nature.

# Appendix III

Age-dependent mortality is assessed uniformly across cohorts (individuals of the same ecotype that are the same age) and is represented by

$$\mu_a = \begin{cases} \nu_a \nu_{1a} a & \text{if } 0 \le a \le a_{max} \\ \infty & \text{if } a > a_{max} \end{cases} \tag{III.1}$$

where $a$ $[d]$ is age and $\nu_a$ $[\frac{1}{d}]$ and $\nu_{1a}$ $[\frac{1}{d}]$ are constants.

Size-dependent mortality is assessed in the model for schooling and non-schooling individuals. For non-schooling individuals, size-dependent mortality is determined by the weight of the individual and is viewed as the mortality due to predation. Size mortality is a function of $m_L + m_S$ and is given by $\mu_w = \nu_w \cdot \mu_{1w} = \nu_w \cdot \mu_{1w}(m_L + m_S)$. $\nu_w$ $[\frac{1}{g}]$ is a constant and $\mu_{1w}$ $[\frac{1}{d}]$ is determined by

$$\mu_{1w} = \begin{cases} v_0 & \text{if } m_L + m_S = 0 \\ v_c & \text{if } w_1 \le m_L + m_S \le w_2 \\ v_f & \text{if } m_L + m_S \ge w_3 \\ \text{continuous and linear} & \text{elsewhere} \end{cases} \tag{III.2}$$

where $v_0$, $v_c$, $v_f$ $[\frac{1}{d}]$ and $w_1$, $w_2$, $w_3$ $[g]$ are all constant parameters.

For schooling individuals, the new size-dependent mortality, referred to as $\mu_{sch}$ $[\frac{1}{d}]$, is a combination of the mortality associated with the size of the individual (from equation (III.2)) and the size of the school which contains the individual under consideration.

The equation for $\mu_{sch}$ is given by

$$\mu_{sch} = g(\rho_{sch})\frac{\mu_{1w}}{n_{sch}} \tag{III.3}$$

where $\mu_{1w}$ is taken from equation (III.2) and $n_{sch}$ is the total number of schools. $g$ is a function of $\rho_{sch}$, the density of the school which contains the individual fish, and is calculated from the following:

$$g(\rho_{sch}) = \frac{d_{sch}}{\rho_{sch} + d_{sch}} \tag{III.4}$$

where $d_{sch}$ [#] is a constant. Notice that as the density of the school becomes large, the value of $g(\rho_{sch})$ becomes smaller and, hence, the mortality for this particular fish also becomes smaller. The maximum possible number of schools is chosen to be 12 based on the difference between the minimum and maximum lengths of individuals in the lake environment such that the smallest difference perceived by an individual is approximately 0.25 inches.

Density-dependent mortality is assessed uniformly across the population, causing $\mu$ to be a nonlinear function of $\rho$. The total biomass, $p_b$ [#], of the population is calculated by summing $(m_L + m_S)_i \cdot \rho_i$ for each characteristic $i$. The density-dependent mortality is then given by

$$\mu_d = \begin{cases} 0.5d_m & \text{if } 0 \leq p_b \leq p_t \\ 0 & \text{if } p_b = p_o \\ d_m & \text{if } p_b \geq p_c \\ \text{continuous and linear} & \text{elsewhere} \end{cases} \tag{III.5}$$

where $d_m$ $[\frac{1}{d}]$ and $p_t$, $p_o$, $p_c$ $[g]$ are all constant parameters. Density-dependent mortality is assessed separately for the lake and ocean populations, however, in both environments it is represented by the same form given in equation (III.5).

Young-of-the-year mortality is also assessed based on the total density, $p_{yoy}$ [#], of the young-of-the-year population. To qualify for young-of- the-year status, the age of the individual must fall between $a_{yoymin}$ $[d]$ and $a_{yoymax}$ $[d]$. Young-of-the-year mortality is calculated using

$$\mu_{yoy} = \begin{cases} 0 & \text{if } 0 \leq p_{yoy} \leq p_{yoy_o} \\ y_m & \text{if } p_{yoy} \geq p_{yoy_c} \\ \text{continuous and linear} & \text{elsewhere} \end{cases} \tag{III.6}$$

where $y_m$ $[\frac{1}{d}]$, $p_{yoy_o}$ [#], and $p_{yoy_c}$ [#] are constant parameters.

# Appendix IV

**C.M. Krohn and C.G. Krohn. Letter to the Editor.** *Applied Energy* **69(3): 239-241, 2001.**

It came to our attention while reviewing the article "Analytical Model of a Residential Desuperheater" by Lee and Jones [125] that the statistical analysis of the designed experiment was fundamentally incorrect. While the use of design of experiments as a tool for sensitivity analysis is a proven and efficient approach, the techniques which afford this efficiency must be understood to draw correct conclusions. The authors use of experimental design is a sound approach to the problem, yet the results point to a much simpler conclusion than the authors recognized.

Lee and Jones use a standard fractional factorial design to analyze the sensitivity of their model to five input parameters, $h_{wtr}$, $h_{refrig}$, $F$, $T_{ri}$, and $T_{wi}$. From this analysis, they conclude that two main effects ($T_{ri}$ and $T_{wi}$), three two-factor interactions ($T_{wi}*h_{refrig}$, $h_{refrig}*F$, and $T_{ri}*h_{refrig}$), and one three-factor interaction ($h_{wtr}*h_{refrig}*F$) all have significant effects on the model output, *desuperheater rate*. For simplicity, we refer to the factors $h_{wtr}$, $h_{refrig}$, $F$, $T_{ri}$, and $T_{wi}$ respectively as A, B, C, D, and E. Table 11 shows the ordering of the high and low levels for each effect in relation to the ordering of other effects. Note that effects which are aliased with each other have identical columns. The alias structure for Lee and Jones' design is given in Table 12. For further explanation on alias structure and fractional factorial designs, see [139].

For each effect to be estimated independently of others, a full factorial is required. While the number of simulations for a two-level, full factorial with five factors is $2^5 = 32$, Lee and Jones' design is a $\frac{1}{4}$ fraction of the full factorial involving eight simulations. Due to the reduction in number of simulations, this design is of resolution $III$, which, in this case, means that each main effect is confounded with at least one two-factor interaction, as well as with other higher-order interactions. This design is commonly referred to as a screening design and can be used only to estimate main effects and possibly one or two specific interactions assuming all other interactions are negligible. A resolution $III$ fractional factorial can also be used as the first step in sequential experimentation. The general methodology behind sequential experimentation is such that a low resolution design is run and analyzed with the results dictating if and which additional fractional factorials are to follow.

In a correct analysis of the output from Lee and Jones' screening design (Lee and Jones' Table 1), it is apparent that no further experimentation is required as the desuperheater model is completely dominated by only two effects, $T_{ri}$ and $T_{wi}$. This can be most simply shown with a least squares model including only these effects:

$$\hat{Y} = 5.6375 + 9.5375(T_{ri}) - 6.3125(T_{wi}) \tag{IV.1}$$

where $\hat{Y}$ represents the predicted response, % error $Q_{desuper}$. Note that these coefficients are in coded units (see p. 283 of [125]) since the actual values for $T_{ri}$ and $T_{wi}$ were not given. The coefficient of determination, $R^2 = 0.999937$, indicates that approximately

99.9937 percent of the variability observed in % error $Q_{desuper}$ is caused by the main effects $T_{ri}$ and $T_{wi}$. Statistically, there is no evidence of any other effect on the response. Notice that three of the interaction effects found to be significant by Lee and Jones are aliased with these two main effects. That is, 9.5375 in (IV.1) actually estimates the sum of the four coefficients for $T_{ri}$, $h_{wtr}{}^{*}F$, $h_{refrig}{}^{*}T_{wi}$, and the five factor interaction. The same idea follows for 6.3125. Our conclusion that the true effects are $T_{ri}$ and $T_{wi}$, as opposed to any of their aliased interactions, is based on the fact that all other main effects are highly insignificant. It is often the case that if interactions are truly significant, the factors that make them up will also show some level of statistical significance as main effects. We make the same assumption with the interaction $h_{refrig}{}^{*}F$, which can be shown as statistically insignificant.

In summary, while Lee and Jones have used an appropriate method for performing a sensitivity analysis, the conclusions drawn cannot be attributed to the statistical experiment used. Their chosen design proved to be the correct one for their problem, with no further experimentation required. However, it has been shown above that Lee and Jones overestimated the number and significance of effects. Had the authors anticipated the importance of several interactions, the 16-run resolution $V$ design, which permits estimation of all main effects and two-factor interactions, would have been useful to avoid having to untangle chains of aliased effects [139].

Table 11: Design matrix for main effects and interactions noted as significant in [125] and reported responses. Note that the levels of the interaction terms are found by taking the product of the factors from which they are composed.

| **A** | **B** | **C** | **D** | **E** | **BC** | **BD** | **BE** | **ABC** | **% error** $Q_{desuper}$ |
|---|---|---|---|---|---|---|---|---|---|
| - | - | - | + | - | + | - | + | - | 21.5 |
| + | - | - | - | + | + | + | - | + | -10.1 |
| - | + | - | + | + | - | + | + | + | 8.7 |
| + | + | - | - | - | - | - | - | - | 2.4 |
| - | - | + | - | + | - | + | - | + | -10.3 |
| + | - | + | + | - | - | - | + | - | 21.5 |
| - | + | + | - | - | + | - | - | - | 2.4 |
| + | + | + | + | + | + | + | + | + | 9.0 |

Table 12: Alias structure for Lee and Jones' fractional factorial. Main effects and interactions found to be significant in [125] are in bold.

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| A | = | CD | = | BCE | = | ABDE |
| B | = | DE | = | ACE | = | ABCD |
| C | = | AD | = | ABE | = | BCDE |
| **D** | = | **BE** | = | AC | = | ABCDE |
| **E** | = | **BD** | = | **ABC** | = | ACDE |
| **BC** | = | AE | = | CDE | = | ABD |
| AB | = | CE | = | ADE | = | BCD |
| Int | = | ACD | = | BDE | = | ABCE |

# PART II

# Iteroparous Reproduction Strategies and Population Dynamics

# 1 Abstract

Asymptotic relationships between a class of continuous partial differential equation population models and a class of discrete matrix equations are derived for iteroparous populations. First, the governing equations are presented for the dynamics of an individual with juvenile and adult life stages. The organisms reproduce after maturation, as determined by the juvenile period, and at specific equidistant ages, which are determined by the iteroparous reproductive period. A discrete population matrix model is constructed that utilizes the reproductive information and a density-dependent mortality function. Mortality in the period between two reproductive events is assumed to be a continuous process where the death rate for the adults is a function of the number of adults and environmental conditions. The asymptotic dynamic behaviour of the discrete population model is related to the steady-state solution of the continuous-time formulation. Conclusions include that there can be lack of convergence to the steady-state age distribution in discrete event reproduction models. The iteroparous vital ratio (the ratio between the maximal age and the reproductive period) is fundamental to determining this convergence. When the vital ratio is rational, an equivalent discrete-time model for the population can be derived whose asymptotic dynamics are periodic and when there are a finite number of founder cohorts, the number of cohorts remains finite. When the ratio is an irrational number, effectively there is convergence to the steady-state age distribution. With a finite number of founder cohorts, the number of cohorts becomes countably infinite. The matrix model is useful to clarify numerical results for population

models with continuous densities as well as delta measure age distribution. The applicability in ecotoxicology of the population matrix model formulation for iteroparous populations is discussed.[1]

## 2 Introduction

In the derivation of structured population dynamic models, a natural and advantageous starting point is the individual level, where physiological processes such as feeding, growth, survival and reproduction are integrated [19]. The aggregate of individuals coupled with representations for the interaction of the individuals with the environment (for example, through food availability, immigration and emigration) form the basis for structured population models. The foundation for the physiologically structured modelling approach is often the McKendrick-von Foerster partial differential equation where a single set of parameters describes the physiological characteristics and the age describes the state of the individuals. The focus here is on the asymptotic dynamics of populations where reproduction occurs as discrete events while death occurs continuously.

Individuals are assumed generally to have three stages, the egg (no feeding or reproduction), the juvenile (feeding but no reproduction) and an adult (feeding and reproduction) stage; however, in this study the egg stage will be dealt with implicitly. Reproduction is assessed in the individual model at discrete ages as proposed by Hal-

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[1] In press with *Bulletin of Mathematical Biology* as "Iteroparous reproduction strategies and population dynamics" by B.W. Kooi, T.G. Hallam, F.D.L. Kelpin, C.M. Krohn, and S.A.L.M. Kooijman.

lam et al. (1990) and is assumed to occur multiple times. All individuals are born with a species specific biovolume and are clones of the parent. In the fixed period between consecutive reproductive events, mortality (also due to harvesting or emigration) is a continuous process. Natural death occurs when an adult reaches the species specific maximum age immediately after their last reproductive event.

Funasaki (1997) performed a simulation study with parameter values realistic for the waterflea *Daphnia magna*. The McKendrick-von Foerster partial differential equation was solved using standard method of characteristics integration techniques with a fixed numerical time-step. The initial population was taken to be one cohort. Depending on the time-step sometimes regular asymptotic dynamics occurred. These simulation results were analysed as time-series where the sampling interval is the numerical time-step. Two methods were considered, namely the Frequency Analysis method by Jenkins and Watts (1968) and the Phase Portrait Reconstruction method developed in [20, 23].

In the frequency analysis method the power spectrum of the time-series was calculated. For some parameter settings, the power spectra showed a dominant frequency corresponding to the length of time between two birth events in the population.

In the phase portrait reconstruction method the basic idea is that lagging one-dimensional time-series data from a dynamical system with itself an appropriate number of times results in the reconstruction of the higher dimensional phase portrait of that system. Total population size time-series data was lagged with itself by the lag equal to the computational time-step and another lag to produce a phase portrait in three dimensions. These three dimensional plots showed a scatter plot at some times and, in other cases, a periodic attractor. The computational time-step played an important role in determining the attractor.

In order to clarify this asymptotic behaviour we investigate a discrete-time nonlinear nonnegative Leslie-matrix equation [17]. Because reproduction occurs as discrete events, there is a discrete-time formalism equivalent to the continuous representation, see [2] (pp. 11) and [3]. Liu and Cohen (1987) obtained a density-dependent matrix by discretizing the continuous time McKendrick-von Foerster model.

Calow et al. (1997) deal with risk assessment on the basis of simplified two-stage life-history model where the individual, if it survives, can potentially breed forever. They develop an approach where they use that model to make explicit and ecologically relevant links between test results at the individual and their implications for population dynamics. The survivorship and the duration of the stages are estimated parameters from individual organism tests. The Euler-Lotka equation gives the impact on the population growth rate, where no density-dependent effects are taken into account.

We employ a technique proposed by Kooi and Boer (1995) who study the dynamics of a worm *Nais elinguis* population consisting of organisms which propagate by binary fission. This population matrix model formulation differs from those proposed in the literature by the choice of the time step and the survivalships in the two stages are derived from continuous time McKendrick-von Foerster model. The exact correspondence between the individual-based population model and the matrix model is possible because of the individual reproductive schedule of iteroparous species where reproduction is pulsed and synchronised.

The paper is organized as follows. An age-dependent density formulation for the dynamics of the physiologically structured population is presented in Section 3.1. In this age-structured formulation, the mathematical model consists of two partial differential equations for the density functions associated with the individual state variables for the two stages: the juvenile and adult stage. The formulation for reproduction provides the boundary condition for the density functions. In Section 3.2, the steady-state age-distribution of the population is derived.

In Section 4, a set of naturally induced age classes, called cohorts, is constructed with the number of individuals in the classes taken as the state variables of the discrete-time model. With these cohorts, the dynamical behavior of the population depends on the ratio between the juvenile period and the reproductive period of the individuals. When this ratio is a rational number, the total biomass of the population can be cyclic when the initial distribution differs from the steady-state density distribution. In this situation, periodic solutions have period equal to the reproductive period divided by the number of cohorts in that period. Furthermore, the number of cohorts with descendants from one founder cohort remains finite.

This natural discrete-time model is compared with the continuous-time model in Section 5. If the ratio is irrational then the dimension of the population projection matrix becomes infinite and the length of the age classes converges to zero, yielding convergence to the steady-state continuous age density distribution. In Section 6 we discuss the applicability of the matrix model formulation in ecotoxicology and risk assessment analysis.

## 3 The Continuous-time Model Formulation

The physiologically structured population model is formulated with a continuous density function describing the number of individuals as it depends on both age and time. The dynamic behavior is described by hyperbolic partial differential equations.

### 3.1 Structured Population Model

In this section we formulate a model to represent a rudimentary life history of an iteroparous species such as *Daphnia*. The life history consists of two stages: the egg and the juvenile stages form the pre-adult stage; the second is the adult stage. The notation used is given in Table 1. Let $m(t, a)$ denote the age-dependent density as a function of time $t$ and age $a$.

At age $a_J$, the individual deposits freshly laid eggs into the brood-pouch for the first time. (Thus, formation of eggs started already at $a_J - a_A$). These eggs hatch at age $a_J + a_A$ and are released in the environment when the mother molts for the second time. The adults molt in a series of instars with a fixed intermolt period. They reproduce by laying eggs in clutches with the development time for the eggs equal to the intermolt period, $a_A$. Thus, offspring are produced at distinct ages from initiation of adulthood, at $a = a_J$, namely at the ages $a_J + sa_A$, $s = 1, \cdots, q$ where $q$ is the number of reproductive events which is assumed to be an integer greater than 1.

With each reproductive event, a fixed number of offspring, the brood-size $r$, is produced. The last reproductive event occurs at the moment the individual attains maximum age $a_M$, thus $a_M = a_J + q\,a_A$. We assume a density-independent mortality rate, $\mu_J$, for the juvenile individuals and density-dependent mortality rate for the adults, $\mu_A(N_A)$, where $N_A$ is the number of adult individuals in the population per unit of volume $N_A(t) = \int_{a_J}^{a_M} m(t,a)\,da$. The equations for the density function $m(t,a)$ are

$$\frac{\partial m}{\partial t} + \frac{\partial m}{\partial a} = -\mu_J m\ , \quad 0 \leq a < a_J\ , \tag{1a}$$

$$\frac{\partial m}{\partial t} + \frac{\partial m}{\partial a} = -\mu_A(N_A)\, m(t,a)\ , \quad a_J \leq a < a_M\ , \tag{1b}$$

$$m(t,0) = r\sum_{s=1}^{q}\int_{a_J}^{a_M}\delta\big(a - (a_J + s\,a_A)\big)m(t,a)\,da = r\sum_{s=1}^{q} m(t, a_J + s\,a_A)\ , \tag{1c}$$

where $\delta$ is the Dirac $\delta$-function. The boundary value for the density function $m(t,0)$ is the population birth rate. Natural death is assessed in the model by the maximum age $a_M$. Continuity conditions for the density function $m(t,a)$ with the transition from juvenile to adult at $a_J$ are imposed.

### 3.2 Steady-state Age Distribution

We assume a constant environment and denote by a superscripted asterisk, $^*$, a steady-state value. An expression for the number of adults in steady-state is $N_A^* = \int_{a_J}^{a_M} m^*(a)\,da$, where $m^*(a)$ is the steady state age distribution. $N_A^*$ is derived using the notion of the net reproductive value, that is the average reproductive output by an individual throughout its entire life span, $R_0$, of the population. Denote the constant death rate for the adults by $\mu_A^* = \mu_A(N_A^*)$. The survival probability for each individual can be characterized by the survival function $S(a)$, defined as the probability that an individual survives and reaches age $a$ [4]. The survival function is given by

$$\frac{dS}{da} = \begin{cases} -\mu_J S(a) \ , & 0 \leq a < a_J \ , \\ -\mu_A^* S(a) \ , & a_J \leq a < a_M \ , \\ -\delta(a - a_M) S(a_M) \ , & a = a_M \ , \end{cases} \tag{2}$$

where $S(0) = 1$. The total number of offspring produced by each individual equals

$$\int_{a_J}^{a_M} \exp\{-\mu_A^*(a - a_J)\} \sum_{s=1}^{q} r\delta\big(a - (a_J + s\, a_A)\big)\, da = \sum_{s=1}^{q} r \exp\{-s\, \mu_A^* a_A\} \ . \tag{3}$$

This number of offspring yields a number of new adults given by

$$R_0(\mu_A^*) = \exp\{-\mu_J a_J\} \sum_{s=1}^{q} r \exp\{-s\, \mu_A^* a_A\} = r \exp\{-\mu_J a_J\} \frac{1 - \exp\{-q\mu_A^* a_A\}}{\exp\{\mu_A^* a_A\} - 1} \ . \tag{4}$$

Necessary for steady-state is $R_0 = 1$, that is, each individual just replaces itself. $R_0$ is a monotonically decreasing function of $\mu_A^*$. For $\mu_A = 0$ we have $R_0(0) = rq \exp\{-\mu_J a_J\}$. We assume that $rq > \exp\{-\mu_J a_J\}$ and this implies $R_0(0) > 1$. For large values of the mortality rate, $\mu_A$, this expression gives $\lim_{\mu_A^* \to \infty} R_0 = 0$. Hence, there is one real root, $\mu_A^*$, of the condition $R_0 = 1$ in (4).

For this steady-state we obtain

$$r\exp\{-\mu_J a_J\}\bigl(1-\exp\{-q\mu_A^* a_A\}\bigr) = \exp\{\mu_A^* a_A\} - 1\ . \tag{5}$$

This equation fixes first the steady-state mortality rate of the adults, $\mu_A^*$, and subsequently the total number of adults in steady-state, $N_A^*$. We assume that the function $\mu_A(N_A)$ has an inverse.

The steady-state age distribution $m^*(a)$ for the juvenile individuals $0 \le a \le a_J$, is given by

$$m^*(a) = m^*(0)\exp\{-\mu_J a\}\ , \tag{6}$$

and for the adults, where $a$ satisfies $a_J \le a < a_M$, it is described by

$$m^*(a) = m^*(0)\exp\bigl\{-\mu_J a_J - \mu_A^*(a-a_J)\bigr\}\ . \tag{7}$$

The last equation of (2) implies that $m^*(a) = 0$ for $a \ge a_M$. The proportionality constant $m^*(0)$ is explicitly given by

$$m^*(0) = \frac{r\mu_A^* N_A^*}{\exp\{\mu_A^* a_A\} - 1}\ , \tag{8}$$

where $\mu_A^*$ is given by (5) and thereafter $N_A^*$ by $\mu_A^* = \mu_A(N_A^*)$. Substitution of (8) in (6) and (7) and subsequently the obtained result in (1c) when (5) is used, shows that this distribution $m^*(a)$ is indeed the steady-state age distribution. The asymptotic distribution for the density need not converge to the derived age distribution $m^*(a)$. To develop this important issue, we now derive a discrete-time formalism equivalent to the continuous model.

## 4 The Discrete-time Model Formulation

We demonstrate that, with a single founder cohort, the dynamics of the continuous model population can be described by a discrete-time nonlinear Leslie-matrix equation. This is a consequence of the fact that the population density may also be described by a sum of delta functions on the space of individual state variable (age) where the dynamic behavior is described by ordinary differential equations.

We define a set of natural age classes for the population as follows. Suppose that $a_A = (l/k)\, a_M$ for some $k, l = 1, \cdots, \infty$ where the vital ratio $k/l$ is in lowest terms and $a_A < a_J$. The age interval $[0, a_M]$ is divided into $k$ subintervals each representing an age class. Each reproductive period $a_A$ is divided into $l$ subintervals such that the age at maturation as well as all ages where reproductive events take place, occur at transitions from one class to an adjacent class. When the juvenile period is a multiple of the reproductive period we have $l = 1$. The adults are in classes determined by intervals $k - ql + 1, \cdots, k$. Now we aggregate the individuals into the classes introduced above. The discrete time-step length will be taken equal to

$$T = a_M/k = a_A/l \ , \tag{9}$$

the duration of the age-classes, and, without loss of generality, time is zero at an instant of reproduction. The number of individuals at time $iT$ in class $j$ with age $(j-1)T < a \leq jT$ is denoted as $n_j^i = n_j(iT)$ and is given by

$$n_j^i = \int_{(j-1)T}^{jT} m(iT, a) \ da \ , \quad i = 1, \cdots, \infty \ , \quad j = 1, \cdots, k \ . \tag{10}$$

With a single founder cohort all individuals are lumped at the left end point of the age interval associated with the cohort. The number of adults at time $iT$, denoted by $N_A^i$, equals $N_A^i = \sum_{j=k-ql+1}^{k} n_j^i$.

The life cycle graph is shown in Figure 1 for $l = 2$ and $k = 11$. At age $a = a_J = 10$ the individual deposits eggs into the brood pouch. These eggs hatch at age $a = a_J + a_A = 14$. This shows that the survival probability in this age class equals that of the adults, $p_A$. Thus, the fertility at that instant, and at the equidistant ages $a_J + sa_A$, $s = 1, \cdots, q$ equals $rp_A$.

Let $\mathbf{n} \in \mathbb{R}^k$ denote the vector with elements given in (10). The autonomous matrix equation for the $k \times k$ population projection matrix, $\mathbf{P}(\mathbf{n^{i-1}})$, reads $\mathbf{n^i} = \mathbf{P}(\mathbf{n^{i-1}})\mathbf{n^{i-1}}$

or

$$
\begin{array}{ccccccccccc}
\multicolumn{3}{c}{|\leftarrow a_J \rightarrow|} & \multicolumn{3}{c}{|\leftarrow a_A \rightarrow|} & \cdots & \multicolumn{3}{c}{|\leftarrow a_A \rightarrow|} \\
\multicolumn{3}{c}{|\quad k-ql \quad|} & \multicolumn{3}{c}{|\qquad l \qquad|} & \cdots & \multicolumn{3}{c}{|\qquad l \qquad|}
\end{array}
$$

$$
\begin{pmatrix} n_1^i \\ \vdots \\ \vdots \\ n_{k-ql+1}^i \\ \vdots \\ n_{k-ql+l+1}^i \\ \vdots \\ \vdots \\ \vdots \\ n_k^i \end{pmatrix}
=
\begin{pmatrix}
0 & \cdots & \cdots & 0 & \cdots & rp_A^{i-1} & \cdots & 0 & \cdots & rp_A^{i-1} \\
p_J & 0 & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & 0 & 0 \\
0 & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \vdots \\
\vdots & \ddots & p_J & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \vdots \\
\vdots & \ddots & \ddots & p_A^{i-1} & \ddots & \ddots & \ddots & \ddots & \ddots & \vdots \\
\vdots & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \vdots \\
\vdots & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \vdots \\
\vdots & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \vdots \\
\vdots & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \ddots & \vdots \\
0 & \cdots & \cdots & \cdots & \cdots & \cdots & \cdots & 0 & p_A^{i-1} & 0
\end{pmatrix}
\begin{pmatrix} n_1^{i-1} \\ \vdots \\ \vdots \\ n_{k-ql+1}^{i-1} \\ \vdots \\ n_{k-ql+l+1}^{i-1} \\ \vdots \\ \vdots \\ \vdots \\ n_k^{i-1} \end{pmatrix}.
\tag{11}
$$

The fraction of the individuals expected to survive and move to the next class after the time step $T$ differs for the juvenile and adult classes

$$p_J = \exp\{-\mu_J T\} \ , \tag{12}$$

$$p_A^{i-1} = \lim_{t \uparrow iT} \frac{N_A(t)}{N_A((i-1)T)} = \lim_{t \uparrow iT} \frac{N_A(t)}{N_A^{i-1}} \ , \tag{13}$$

where

$$\frac{dN_A}{dt} = -\mu_A(N_A)N_A \ , \qquad (i-1)T \leq t < iT \ . \tag{14}$$

We used the fact that (by choice of the time step) no adult reaches the maximum age $a_M$ and no juvenile individual matures within each projection interval of length $T$, and that the mortality rate is age-independent.

Reproduction of $r > 0$ offspring occurs in the classes $k-(s-1)l$, with $s = 1, \cdots, q$. So, there are $q$ nonzero elements in the first row of the $k \times k$ matrix at positions $(1, k-sl)$, $s = 0, \cdots, q-1$ and the fertility is $rp_A$. Because the survival probability $p_A$ depends on the total number of adults, the matrix equation (11) is nonlinear.

## 4.1 Linear Model

Suppose that the mortality rate of the adults $\mu_A$ is independent of $N_A$. Then, equation (11) is a linear autonomous nonnegative matrix with constant $p_A^{i-1} = p_A$ where

$$p_A = \exp\{-\mu_A T\} \ . \tag{15}$$

The resulting nonnegative population matrix will be denoted by $\mathbf{P}$. The characteristic equation, $\det(\alpha\mathbf{I} - \mathbf{P}) = \mathbf{0}$, often called the Euler-Lotka equation for the matrix equation (11), is

$$r \exp\big\{-(\mu_J - \mu_A)a_J\big\} \sum_{s=0}^{q-1} \alpha^{-(k-sl)} \exp\big\{-(k-sl)\mu_A T\big\} = r p_J^{k-ql} \sum_{s=1}^{q} \alpha^{-(k-(q-s)l)} p_A^{sl} = 1\ , \tag{16}$$

where $\alpha$ is a characteristic value (eigenvalue) of $\mathbf{P}$. The column eigenvector equals

$$\mathbf{n} = \begin{pmatrix} \alpha^{k-1} \\ \alpha^{k-2} p_J \\ \vdots \\ \alpha^{ql-1} p_J^{k-ql} \\ \alpha^{ql-2} p_J^{k-ql} p_A \\ \vdots \\ p_J^{k-ql} p_A^{ql-1} \end{pmatrix} = \begin{pmatrix} \alpha^{k-1} \\ \alpha^{k-2} \exp\{-\mu_J T\} \\ \vdots \\ \alpha^{ql-1} \exp\{-(k-ql)\mu_J T\} \\ \alpha^{ql-2} \exp\big\{-(\mu_J - \mu_A)a_J - (k-ql+1)\mu_A T\big\} \\ \vdots \\ \exp\big\{-(\mu_J - \mu_A)a_J - (k-1)\mu_A T\big\} \end{pmatrix} . \tag{17}$$

When $q = 1$, semelparous species [12] are represented and individuals die immediately after they reproduce. We assume in the sequel that $q > 1$. The case $q = 2$ is considered in Kooi and Boer (1995) who develop a discrete-time model for species which proliferate by binary fission into two unequal sized new-borns.

The right top element of the matrix is $rp_A > 0$ since post-reproductive classes are excluded, and this implies that the population matrix is irreducible. The life cycle graph, Figure 1, is strongly connected as there is a path in the graph from every node to every other node [2] (pp. 58).

The population matrix is also primitive. The greatest common divisor of the integers $(k-(k-l),(k-l)-(k-2l),\cdots,(k-(q-1)l)-(k-ql),k-ql)=(l,l,\cdots,l,k-ql)$ equals 1 and therefore the matrix is primitive, using the Euler-Lotka equation (16), the definition of $l$ and $k$ by $a_M/k=T$ and [7] (Vol. 2). (It should be mentioned that in [3] the last term $k-ql$ is missing.) Primitiveness can also be derived from the life cycle graph. For example in Figure 1, the lengths of its loops in the life cycle graph are $(k,k-l,\cdots,k-(q-1)l)$; the greatest common divisor of these lengths is 1 and, therefore, the population matrix $\mathbf{P}$ where $p_A^{i-1}=p_A$ given in (15) is primitive [2].

Thus, the nonnegative population matrix $\mathbf{P}$ is irreducible and primitive and therefore the Perron-Frobenius theorem applies [2]. Hence, there is a dominant real eigenvalue denoted by $\alpha^*>0$ and there is convergence to the strictly positive eigenvector (17) associated with this dominant positive real eigenvalue whether the projection matrix is diagonalizable or nondiagonalizable [3].

### Steady-state

When the dominant eigenvalue is equal to one, $\alpha^*=1$, with $a_J=(k/l-q)a_A$ and $a_A=lT$, the characteristic equation (16) is the condition $R_0=1$ in equation (4) for the continuous-time formalism. Consequently a real $\mu_A=\mu_A^*$ exists and is again given by (5). The Euler-Lotka equation (16) can be rewritten with $\alpha = 1$

$$R_0(\mu_A) = r \exp\big\{ -\mu_J a_J \big\} \sum_{s=1}^{q} \exp\big\{ -slT\mu_A \big\} = r p_J^{k-ql} \sum_{s=1}^{q} p_A^{sl} \, . \tag{18}$$

The column eigenvector (17) associated with the dominant eigenvalue $\alpha^* = 1$ is just the survival function for a single individual

$$\mathbf{n}^* = \begin{pmatrix} 1 \\ \exp\{-\mu_J T\} \\ \vdots \\ \exp\{-\mu_J a_J\} \\ \exp\{-\mu_J a_J - \mu_A^* T\} \\ \vdots \\ \exp\{-\mu_J a_J - (ql-1)\mu_A^* T\} \end{pmatrix} . \tag{19}$$

This vector is proportional to the continuous-time age distributions (6) and (7) where the distinct ages $a = jT$, $j = 0, \cdots, k-1$ are substituted.

Depending on whether the mortality rate of individuals is greater, smaller or equal to $\mu_A^*$, the population increases infinitely ($R_0 > 1$), goes to extinction ($R_0 < 1$) or remains constant ($R_0 = 1$). There is, however, always convergence of the discrete-time distribution to the eigenvector (19) when there is a single founder cohort. With $\mu_A = \mu_A^*$ ($R_0 = 1$) the discrete-time steady-state is neutral stable.

### Cyclic Continuous-time Behaviour

Now we assume that the discrete-time distribution converges to the eigenvector (19), the discrete-time steady-state distribution, and derive the time-dependency between two reproductive events. Let $\tau \in [0, T)$ denote the time since a reproductive event. For $\tau = 0$, the total number of adults in the discrete-time model is given by $N_A(0) = N_A^*$ (recall that for the linear case this number is not fixed, but depends on the initial number). Since there is no reproduction within each time interval, the time-variation of the number of adults in the time interval $\tau \in [0, T)$ is given by the ODE

$$\frac{dN_A}{d\tau} = -\mu_A^* N_A \ , \tag{20}$$

with initial condition for $\tau = 0$, $N_A(0) = N_A^* = \sum_{j=k-ql+1}^{k} n_J^*$. Between two reproductive events for the discrete-time steady-state, the solution of this ODE reads

$$N_A(\tau) = N_A^* \exp\{-\mu_A^* \tau\} \ . \tag{21}$$

Hence, the continuous-time solution for the total number of adults, compatible with the discrete-time steady-state, is periodic with period equal to $T$.

## 4.2 Nonlinear Model

In this section we analyse the local stability of the steady-state of the nonlinear projection matrix for the density-dependent population. We follow the technique proposed in [2, 21, 22].

For purposes of analysis, the per capita mortality rate, $\mu_A(N_A)$, is assumed to be

$$\mu_A(N_A) = \mu_A^* + \nu_A(1 - \frac{N_A}{\overline{N}_A}) \ , \tag{22}$$

where $\mu_A^*$ is given by (5), $\nu_A$ is a constant, positive or negative such that $\nu_A = 0$ is the linear case. The parameter $\overline{N}_A$ is determined by environmental conditions.

For a fixed value of $\nu_A$, there is a one-to-one correspondence between the mortality rate and the number of adults. Since the mortality rate is age-independent, the time-dependency of the total number of adults, $N_A(t)$, in each time interval $(i-1)T \leq t < iT$ is described by the ordinary differential equation

$$\frac{dN_A}{dt} = -\mu_A^* N_A - \nu_A(1 - \frac{N_A}{\overline{N}_A})N_A \ , \tag{23}$$

with initial condition for $t = (i-1)T$, $N_A((i-1)T) = N_A^{i-1}$.

Equation (23) is the logistic equation

$$\frac{dN_A}{dt} = \beta(1 - \frac{N_A}{K})N_A \ , \tag{24}$$

however, the growth rate can be negative in our formulation, namely $\beta = -(\mu_A^* + \nu_A)$. The carrying capacity is now interpreted as the asymptotic value for $N_A(t)$ when $t \to \infty$.

If there is no reproduction, then

$$K = \lim_{t\to\infty} N_A(t) = \frac{(\mu_A^* + \nu_A)\overline{N}_A}{\nu_A} \ . \tag{25}$$

In the linear case, where $\nu_A = 0$, that the asymptotic value is zero follows from solving (23).

We consider again the one founder cohort case. Because there is no reproduction within each time interval, the number of adults in the time interval $t \in [(i-1)T, iT)$ is obtained by integration of the equation (23) and equals

$$N_A(t) = \begin{cases} \frac{(\mu_A^*+\nu_A)\exp\{-(\mu_A^*+\nu_A)(t-(i-1)T)\}N_A^{i-1}}{\mu_A^*+\nu_A+\nu_A\left(\exp\{-(\mu_A^*+\nu_A)(t-(i-1)T)\}-1\right)N_A^{i-1}/\overline{N}_A} & , \quad \nu_A \neq -\mu_A^* \ , \\ \frac{N_A^{i-1}}{1+\mu_A^*(t-(i-1)T)N_A^{i-1}/\overline{N}_A} & , \quad \nu_A = -\mu_A^* \ . \end{cases} \tag{26}$$

Thus the survival probability $p_A^{i-1} = \lim_{t\to iT} N_A(t)/N_A^{i-1}$ is given by

$$p_A^{i-1}(N_A^{i-1}) = \begin{cases} \frac{(\mu_A^*+\nu_A)\exp\{-(\mu_A^*+\nu_A)T\}}{\mu_A^*+\nu_A+\nu_A\left(\exp\{-(\mu_A^*+\nu_A)T\}-1\right)N_A^{i-1}/\overline{N}_A} & , \quad \nu_A \neq -\mu_A^* \ , \\ \frac{1}{1+\mu_A^* T N_A^{i-1}/\overline{N}_A} & , \quad \nu_A = -\mu_A^* \ . \end{cases} \tag{27}$$

Hence, the density-dependent function is of the *compensatory* or Beverton-Holt type, see [21], [2] (pp. 232). For a fixed value of $\nu_A$, the survival probability is a function of $N_A$ and decreases monotonically toward zero from a maximum at $N_A = 0$.

### Extinction Steady-state

In the extinction steady-state the number of organisms is zero. This trivial steady-state is denoted by $\widetilde{}$. In this steady-state, the Jacobian equals the population projection matrix, called the *inherent projection matrix*, see (1a). At the extinction steady state, the density effects are unimportant and therefore the population projection matrix governs the dynamics at low population levels, see also [3]. The mortality rate is given by

$$\widetilde{\mu}_A = \mu_A^* + \nu_A \ , \tag{28}$$

and the survival probability $\widetilde{p}_A = \lim_{t \to iT} N_A(t)/N_A^{i-1}$ is given by

$$\widetilde{p}_A(\nu_A) = \exp\{-(\mu_A^* + \nu_A)T\} \ , \quad \nu_A \neq -\mu_A^* \ . \tag{29}$$

Because the function $R_0(\mu_A)$ defined in (18) is monotonically decreasing and $R_0 = 1$ for $\nu_A = 0$, we conclude that for $\nu_A > 0$, we have $R_0 < 1$ and the extinction steady-state is stable. For $\nu_A < 0$ we have $R_0 > 1$ which implies instability and invasibility because the number of individuals increases when rare. When $\nu_A < -\mu_A^*$, the mortality rate is negative and loses its biological interpretation. Instability of the extinction steady-state for this case is immediate.

**Positive Steady-state**

We denote by $\widehat{\ }$ the nontrivial, positive steady-state. The reproductive output by an average individual throughout its entire lifespan, with density-dependent mortality as in (22), is

$$R_0(\widehat{p}_A) = rp_J^{k-ql} \sum_{s=1}^{q} \widehat{p}_A^{\,ls} = r\exp\{-\mu_J a_J\}\widehat{p}_A^{\,l} \frac{1-\widehat{p}_A^{\,lq}}{1-\widehat{p}_A^{\,l}} \ , \tag{30}$$

where $R_0 = 1$ gives the steady-state. In the previous section we showed that for $rq > \exp\{-\mu_J a_J\}$, $\mu_A^* > 0$ exists. In a similar way we show that for $rq > \exp\{-\mu_J a_J\}$, $0 < \widehat{p}_A < 1$ exists and is unique. As a result, the survival probability in the positive steady-state equals the survival probability for the linear steady-state ($\widehat{p}_A = \exp\{-\mu_A^* T\}$) and, consequently, it does not depend on $\nu_A$.

By substitution in the population projection matrix equation (11), it can be shown that the discrete-time positive steady-state distribution is proportional to

$$\widehat{\mathbf{n}} = \begin{pmatrix} 1 \\ \exp\{-\mu_J T\} \\ \vdots \\ \exp\{-\mu_J a_J\} \\ \exp\{-\mu_J a_J\}\,\widehat{p}_A \\ \vdots \\ \exp\{-\mu_J a_J\}\,\widehat{p}_A^{\,ql-1} \end{pmatrix} \ , \tag{31}$$

where $\widehat{p}_A = p_A(\widehat{N}_A)$. The proportionality constant is such that $\widehat{N}_A = \sum_{j=k-ql+1}^{k} \widehat{n}_J$. This property is a result of the fact that the density-dependence affects the fertilities and survival probabilities for the adults equally, since $p_A^{i-1}$ given in (27) is equal for all adult age-classes. This positive steady-state distribution is again the survival probability function for a single individual.

Thus, the discrete-time positive steady-state distribution $\widehat{\mathbf{n}}$ in (31) equals $\mathbf{n}^*$ in (19).

Substitution of $\widehat{p}_A$ in (27) gives an explicit expression for $\widehat{N}_A$

$$\widehat{N}_A = \begin{cases} \overline{N}_A \frac{(\mu_A^* + \nu_A)(\exp\{-(\mu_A^* + \nu_A)T\} - \widehat{p}_A)}{\widehat{p}_A \nu_A \left(\exp\{-(\mu_A^* + \nu_A)T\} - 1\right)} & , \quad \nu_A \neq -\mu_A^* \ , \\ \overline{N}_A \frac{1 - \widehat{p}_A}{\widehat{p}_A \mu_A^* T} & , \quad \nu_A = -\mu_A^* \ . \end{cases} \tag{32}$$

The stability properties of this positive steady-state are determined by the eigenvalues of the linear approximation matrix

$$\mathbf{P}|_{\widehat{\mathbf{n}}} + \sum_{\mathbf{j=k-ql+1}}^{\mathbf{k}} \frac{\partial \mathbf{P}}{\partial \mathbf{n_J}}\Big|_{\widehat{\mathbf{n}}} \mathbf{H_J} \ , \tag{33}$$

where $\mathbf{H_J}$ has $\widehat{\mathbf{n}}$ in column $j$ and zeros elsewhere. The partial derivative $\frac{\partial \mathbf{P}}{\partial n_J}$ is only nonzero for the elements of $\mathbf{P^{i-1}}$ equal or proportional to $p_A^{i-1}$; see (11). The partial derivative of $p_A^{i-1}$ (27), with respect to each element of the population vector evaluated in steady-state given by (31), equals zero for $i > 0, j = 1, \cdots, k - ql$. For $\nu_A \neq -\mu_A^*$

and $i > 0, j = k - ql + 1, \cdots, k$ we have

$$\frac{\partial p_A^{i-1}}{\partial n_j}\Big|_{\widehat{\mathbf{n}}} = -\frac{(\mu_A^* + \nu_A)\exp\{-(\mu_A^* + \nu_A)T\}\nu_A(\exp\{-(\mu_A^* + \nu_A)T\} - 1)}{\overline{N}_A\big(\mu_A^* + \nu_A + \nu_A(\exp\{-(\mu_A^* + \nu_A)T\} - 1)\widehat{N}_A/\overline{N}_A\big)^2}\,. \tag{34}$$

A similar expression holds for $\nu_A = -\mu_A^*$. When the magnitude of the eigenvalues of the resulting approximation matrix is less than 1, the steady-state is stable.

### Bifurcation Analysis

Bifurcation analysis is used to study the stability of the trivial and non-trivial steady-states of the nonlinear model. Figure 2 shows the one-dimensional bifurcation diagram with the bifurcation parameter $\nu_A$. The steady-state ratio of the number of adults $\widehat{N}_A/\overline{N}_A$ is depicted as a function of the bifurcation parameter $\nu_A$ calculated with (32) where the parameter values are listed in Table 1.

For $\nu_A = 0$, the positive steady state $\widehat{N}_A$ depends on the initial value $N_A(0)$ and is neutral stable. For $\nu_A < 0$, the positive steady-state $\widehat{\mathbf{n}} \in {\mathbb{R}_+}^k$ is stable and the extinction steady-state solution $\widetilde{\mathbf{n}} = \mathbf{0}$ is unstable. For $\nu_A > 0$, the positive steady-state is unstable and the extinction steady-state solution is stable. Equation (32) implies that $\widehat{N}_A > \overline{N}_A$, and therefore, the mortality rate $\mu_A$ becomes negative for large values of $\nu_A$. This yields that the positive steady-state is unstable. Computer simulations suggest that the population goes extinct starting with positive values $\mathbf{n}(\mathbf{0}) \in {\mathbb{R}_+}^k$.

Generally, the asymptotic rate of convergence is the largest magnitude of the eigenvalues of the Jacobian evaluated in the steady-state. In Figure 3, these eigenvalues are shown in the complex plane for two values: $\nu_A = 0$ and $\nu_A = -4$. For $\nu_A = 0$, we have the linear case and the Jacobian equals the population projection matrix. The dominant eigenvalue $\alpha^* = 1$ and all the other eigenvalues lie inside the unit circle. There is no convergence to the steady-state in that the number of adults does not converge and the steady-state is neutrally stable. However, the distribution converges to the steady-state distribution and the rate of convergence is the ratio of magnitudes of the second largest absolute magnitude and the largest magnitude, $\alpha^* = 1$, of the eigenvalues of the population projection matrix [2].

The calculated values for $\nu_A = -4$ show that the real eigenvalue is almost zero but the complex conjugate pairs do not differ much from the linear case. This shows that the rate of convergence is fast only starting from a perturbation along the eigenvector belonging to the real eigenvalue, but from other perturbations of the steady-state, the rate of convergence is low.

### Cyclic Continuous-time Behaviour

Similar to the linear model case, the asymptotic continuous-time solution for the number of adults $N_A(t)$ is periodic with period $T$. Figure 4 shows the periodic behaviour for $\nu_A = 0$ (the linear case) and $\nu_A = -4$ (the nonlinear case) with the parameter values listed in Table 1. In the discrete-time steady-state situation, during the projection interval, $T$, the number of adults starts at $\widehat{N}_A$ and diminishes to $\widehat{p}_A \widehat{N}_A$ at the end of the period. It is then increased step-wise to $\widehat{N}_A$ again because of the pulsed reproduction, indicating the periodic solution.

In the nonlinear case, the vector (31) is not proportional to the continuous-time age distributions $m^*(a)$ (6) and (7) where the distinct ages $jT$, $j = 0, \cdots, k-1$ are substituted as was the case in the linear model. This is a result of the fact that the density-dependent mortality rate is periodic as is the solution. With the continuous-time steady-state, the number of adults is constant. This forces equivalence for the linear case where the survival probability function is an exponential decay function. Consequently, within the time intervals, the total number of adults also decays exponentially. For the nonlinear density-dependent case, the survival function is no longer an exponential decay function, but is given in (26) and shown in Figure 4.

Finally, we consider the following formulation of the mortality rate

$$\mu_A(N_A) = \mu_A^* + |\nu_A|(1 - \frac{N_A}{\overline{N}_A}) \ . \tag{35}$$

This density-dependent mortality rate is similar to the one used in [6]. The one-dimensional bifurcation diagram for $\nu_A > 0$ is the mirror image of that for $\nu_A < 0$ since (32) implies $\widehat{N}_A > \overline{N}_A$ for the positive steady-state. Hence, the positive steady-state is stable, except for $\nu_A = 0$, where it is neutrally stable. The limiting value for $\nu_A = 0$ with $\widehat{p}_A = \exp\{-\mu_A^* T\}$ using (32) is

$$\widehat{N}_A = \overline{N}_A \frac{\mu_A^* T}{1 - \exp\{-\mu_A^* T\}} \ . \tag{36}$$

# 5 Comparison of the Natural Discrete-time and the Continuous-time Models

Generally, the population density distribution can be taken to be any distribution, including the steady-state continuous-time age distribution, a uniform distribution within each age class, and the measure distribution with a finite number of cohorts. In the latter case, the dynamics of the whole system is described by a set of ordinary differential equations; namely, for each cohort, one differential equation is formulated with the number of individuals as a dependent variable.

The results obtained for the one founder cohort case in the previous section for a single founder cohort can be elucidated using the notion of the torus $\mathbf{T^2}$. The length of the centre-line of the torus in the long direction is $a_M$ and along the torus in the short direction is $a_A$. Suppose $a_A = 4$, $a_J = 10$, and the number of reproductive events is $q = 3$; thus, $a_M = a_J + 3a_A = 22$. Then $a_A/a_M = 2/11$, thus $k = 11$ and $l = 2$. After $l = 2$ revolutions along the centre-line of the torus in the long direction accompanied by $k = 11$ revolutions along the torus in the short direction, the orbit continues along the path travelled the time $2a_M = 11a_A$ ago, showing periodicity. In Figure 5, the trajectory of an individual is followed for this simple case.

In general, when the ratio of the reproductive period, $a_A$, and the juvenile period, $a_J$, is rational, $a_A/a_J \in \mathbb{Q}$, after $l$ revolutions along the centre-line of the torus in the long direction accompanied by $k$ revolutions along the torus in the short direction, the orbit continues along the path travelled the time $la_M = ka_A$ ago. This shows that when all individuals have one common ancestor, only a finite number of cohorts exist, namely $k$. Offspring from different generations of the founder cohort are produced at the same time and combine into a single cohort leading to the finite number of cohorts.

If there are a finite number of founder cohorts, then the total number of individuals is obtained by superposition of the solutions for each founder cohort, all are of the same period, but are out of phase. For $l = 2$ and $k = 12$, $T = a_A/2 = 2$, the life cycle graph is shown in Figure 6. There are two founder cohorts one starting with $a = 0$ and the second with $a = 2$ at $t = 0$. The reproductive events occur at $a = 16, 20, 24$ for both cohorts.

In Figure 7, the eigenvalues are shown in the complex plane for $\nu_A = 0$ (linear case) and the eigenvalues of the linear approximation matrix for $\nu_A = -4$ (nonlinear case). For $\nu_A = 0$, the population projection matrix is cyclic with index of imprimitivity $l = 2$. There is an eigenvalue which is in steady-state equal to one, $\alpha^* = 1$ with the eigenvector given in (31). However, there is also an eigenvalue $\alpha = -1$. All other eigenvalues are inside the unit circle.

The eigenvector belonging to $-1$ equals that eigenvector belonging to 1 of the matrix $\mathbf{P^2}$. This matrix is built up with 2 uncoupled graphs, see Figure 6. After re-ordering, the full population projection matrix is built up with 2 projection matrices on the diagonal. Both have the same structure as the projection matrix with $l = 1$ and $k = 6$, where $T = a_A = 4$ and the same Euler-Lotka equation (16) holds as for the projection matrix $\mathbf{P}$ itself. This can be explained as follows. Let the time between two observations be equal to the period between two reproductive events $a_A$. The life cycle graph separates now into two independent sub-graphs. These are the life cycle graphs for the two founder cohorts with ages at $t = 0$ equal to $a = 0$ and $a = 2$ while aging and the reproduction strategy is the same. The survival probabilities and fertilities of the two corresponding matrices are indicated in Figure 6. As a consequence, steady-state occurs under the same conditions. Hence, the eigenvector evaluated at this steady-state belonging to eigenvalue $\alpha^* = -1$ is the vector formed by merging the eigenvectors belonging to eigenvalue 1 of these two matrices evaluated in this steady state, however, with different signs

$$\mathbf{n}_{\alpha^*=-\mathbf{1}} = \begin{pmatrix} 1 \\ -\exp\{-\mu_J T\} \\ \vdots \\ \exp\{-\mu_J a_J\} \\ -\exp\{-\mu_J a_J - \mu_A^* T\} \\ \vdots \\ -\exp\{-\mu_J a_J - (ql-1)\mu_A^* T\} \end{pmatrix} . \tag{37}$$

In general, the index of imprimitivity is $l$ and there are $l-1$ complex eigenvalues with magnitude 1, whose values are given by $\exp\{u/l\ 2\pi i\}$, $u = 1, 2, \cdots, l-1$, Caswell (1989) indicating that there is no convergence.

With multiple founder cohorts there is no direct interaction between descendants of different founder cohorts. As a result, there is no convergence to the discrete-time age distribution (31), when $a_A/a_J \in \mathbb{Q}$. The cyclic behaviour depends on the initial conditions, that is, the positive steady-state is neutrally stable.

For the density-dependent mortality case, a similar approach is impossible because the mortality rate depends on the number of adults which changes at every time step. However, the life cycle graphs shown in Figure 6 remain valid. Thus, also for density-dependent mortality case, with multiple founder cohorts there is no direct interaction between descendants of different founder cohorts. The calculated values for $\nu_A = -4$, also shown in Figure 7, reveal that one real eigenvalue of the Jacobian evaluated in the steady-state equals $-1$, indicating that there is no convergence. The Jacobian given in (33) is the sum of two matrices of which the first term is just the population matrix itself and is therefore imprimitive. The second term gives the interaction between descendants of different founder cohorts via the density-dependent mortality rate. However, the descendants of different founder cohorts are still born at different times. Thus, the individuals in one age class have one common ancestor.

With a continuous age distribution and $a_A/a_J \in \mathbb{Q}$, there is no convergence within a class, and only the distribution of the total number of individuals in the classes converges to an asymptotic distribution. As an example, when the continuous age distribution in a class is uniform, it is uniform after each reproductive period $a_A$, and does not converge to the steady-state age distribution, $m^*(a)$. The values of the uniform distribution within the classes change and converge to values so that the total number of individuals in the classes converge to the discrete-time age distribution values. This is a result of the fact that offspring are produced at the same time by multiple adult classes which gives a mixing among the age classes with respect to total numbers. Within the age classes, there is no mixing, and, therefore, there is no convergence.

When the ratio is irrational so that $a_A/a_J \notin \mathbb{Q}$, the orbit is not periodic on the torus; hence, the map never closes on itself. The origin is never intersected again, however, it is an accumulation point for the set of intersections, see [8, 16]. The intersection points are dense in the horizontal axis $[0, a_M]$ as in the Poincare section of the torus. As time goes to infinity, the orbit on the torus will eventually come arbitrarily close to every point on the toroidal surface. This gives a countable infinite number of cohorts as time goes to infinity.

With $a_A/a_J \notin \mathbb{Q}$, the dimension of the population projection matrix is infinite. Therefore we consider a series $l_n/k_n$ with $l_n, k_n \to \infty$ for $n \to \infty$ such that this series of rational numbers converges to the irrational ratio. Then, the length of the age interval of the classes converges to zero, since $T = a_A/l$. Equations (30) and (5) yield

$$\widehat{p}_A = \exp\{-\mu_A^* a_A/l\} \approx 1 - \mu_A^* T \ , \tag{38}$$

where we retained the first order approximation with respect to small $T$. Substitution of this result in (32) gives the following approximating expression for $\widehat{N}_A$

$$\widehat{N}_A \approx \frac{\overline{N}_A}{1 - \mu_A^* T} \ . \tag{39}$$

Therefore we effectively have convergence to a infinite number of cohorts dense with respect to the continuous-time age distribution and the number of adults is close to $\overline{N}_A$.

## 6 Discussion and Conclusions

In [9], populations with both continuous (death) and discrete (reproduction) elements are investigated as we do here. The dynamics of the population with pulsed reproduction are formulated by a difference equation for one state variable, namely the population size. The influence of the environment is taken into account as a density-dependent within-season mortality. This formulation is appropriate for simple ecological systems of seasonally breeding populations with non-overlapping generations.

Huyer (1997) studies the asymptotic behavior (existence and stability) of a similar type of model, also incorporating discrete event reproduction, where growth is again limited by resource availability. The population consists of a finite number of cohorts. Here the individuals die immediately after they reproduce as do semelparous species such as *Oikopleura*, salmon, eel and most cephalopods.

The work here differs from Gyllenberg's and Huyer's in that the population is iteroparous, that is the individuals reproduce more than once, and die immediately after the last reproductive event. There is a juvenile period in which there is no reproduction and there are overlapping generations. The waterflea *Daphnia* has this type of life history. Furthermore, we consider continuous densities as well as delta measures (spikes, each spike representing a cohort) for the age distributions for the population.

When the individuals do not die immediately after the last reproductive event, introduction of a post-reproductive class affects only the density-dependent mortality rate defined in (22) while all other parameters and the analysis of the model remain unchanged. Notice that the analysis would be much easier when the density affects all the vital rates equally [2] (pp. 243), that is, when the mortality depends on the total number of individuals and not only the number of adults.

In the literature, see for instance [9, 14], a relationship between the period of population cycles and the type of density-dependence is made. Here the period depends just on two life-history parameters.

Due to the discrete reproduction events in the physiologically structured populations studied in this paper, there is not always convergence to the steady-state continuous-time age distribution. When the iteroparous vital ratio of the juvenile period and reproduction period is rational, there is no convergence to the steady-state continuous-time age distribution. In this situation, the results obtained with the discrete-time formalisms can be used to clarify results for the continuous-time representation. With one founder cohort, the number of cohorts remains finite and there is convergence to a stable discrete-time age distribution when the mortality rate is density-dependent. Reproduction at the same moment by multiple adult age classes yields a mixing among the age classes with respect to the total number of individuals in the classes. There is no mixing within an age class and, therefore, there is no convergence. This implies periodicity for the continuous-time age distribution and number of adults. With multiple founder cohorts, again there is no convergence to the steady-state age distribution but there is periodicity.

When the ratio between the juvenile period and reproduction period is irrational, effectively there is convergence to the steady-state continuous-time age distribution. With a finite number of founder cohorts, there are asymptotically a countable infinite number of cohorts and the length of the age classes goes to zero. For a similar case in [16] it was shown that the convergence rate can be small. This resembles the continuous reproduction case (often used in the literature) with complete mixing, where at each time, all adults contribute to the formation of offspring, giving convergence to the steady-state age distribution.

With the continuous-time steady-state age distribution the number of adults is time-invariant and equals the value $\overline{N}_A$. Only when $a_A/a_J \notin \mathbb{Q}$ for the density distributions as well as measure distributions there is effectively convergence to the steady-state age distribution and the same applies.

In [5], the relationships between the various discrete- and continuous-time models for the dynamics of physiologically structured populations are elucidated. A numerical scheme for the solution of physiologically structured populations is derived from the Leslie matrix model. In that formulation, no juvenile period was assumed and therefore the time step was equal to the fixed time period between two consecutive reproduction events. In this paper there is a juvenile period and its length together with the reproductive period determine the projection time interval in the Leslie matrix.

To solve the age structured McKendrick-von Foerster equation (1) Funasaki (1997) used integration along the characteristics with a fixed time step. When the reproductive period is a multiple of the time step chosen, an equivalent Leslie matrix model formulation is possible. It was found that in those cases the solution is periodic as predicted by the discrete-time model developed here. As a result of the juvenile period, the projection interval is, however, not the time period between two consecutive reproduction events. The period of the cyclic behaviour generally is not the generation time, but is equal to the reproductive period divided by the number of cohorts in that period. This agrees with the results obtained in [6] based on time-series analyses.

Often the solution of the governing equations have to be approximated using numerical techniques. Roundoff errors on digital computers imply working with rational numbers. The dimension of the population matrix will be large and hence the corresponding fluctuations are of the order of the roundoff error and therefore imperceptible. More important are truncation errors generally made with the finite discretisation of differential equations whereby often “nice” equidistant grid meshes are chosen in order to facilitate the study of convergence of the numerical scheme. Furthermore, due to large experimental errors or the biological stochasticity, measured vital parameter values are often truncated to numbers with a few significant digits. As a result, this involves lumping of individuals into finite cohorts yielding no convergence to the steady-state age-distribution. The presented discrete-time model can be used to clarify obtained numerical results.

In nature, the juvenile period as well as the reproduction period are subject to biological stochasticity, and as a consequence, so is their ratio. Then, mixing among the age classes is expected, yielding convergence to the steady-state age distribution. Therefore, the steady-state age distribution based on estimated values for the juvenile period, reproduction period, number of reproductive events during lifetime and the brood size gives a good approximation for the long-term behaviour for a population when there are initially a large number of individuals not belonging to a small number of distinct cohorts. The steady-state distribution, then often called "stable age distribution", assumption is made with the derivation of stage-classified matrix models [2] (pp. 45) used for risk assessment analyses. Each life-history stage (juvenile, adult) is described by the number of individuals in that stage. The elements on the diagonal of the population projection matrix are the proportions of individuals that remain in the same stage during a time step and the sub-diagonal elements the proportions that go to the next stage.

In ecotoxicology, predictions from ecotoxicity tests on individual organisms are made about the effects of environmental stress from both biological (predators) or anthropogenic sources (chemical concentrations) on population dynamics. In many ecological studies, see for instance [1], a negative growth rate of the population leads to extinction. This is in agreement with the result for density-independent (linear) mortality rate where the discrete-time steady-state is neutral stable. In [10, 15] the change of the juvenile period and the reproduction period of the waterflea *Daphnia* due to an environmental stress perturbation is dealt with. The population matrix model formulation for iteroparous species (such as *Daphnia*), proposed here can be used to investigate the effects of the changes in these two life-history parameters on the population dynamics. In a subsequent risk assessment this and other stress effects can be translated into consequences for population extinction.

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# Appendix

Table 1: List of symbols. The symbols in the column labelled 'dimension' stand for: # number of individuals, t time, v volume of environment. We took $\mu_J = \mu_A^*$ where $\mu_A^*$ is the root of (5). The parameter values in the last but one column are for analysis purpose. More biologically realistic values are given in the last column.

| Symbol | Dimension | Interpretation | Values | Values |
|---|---|---|---|---|
| $a$ | t | Age | | |
| $a_J$ | t | Juvenile period | 10 | 8.3 |
| $a_A$ | t | Reproductive period | 4 | 4 |
| $a_M$ | t | Maximum age | 22 | 48.3 |
| $m(t,a)$ | $\#\,\mathrm{t}^{-1}\,\mathrm{v}^{-1}$ | Population density | | |
| $N_J$ | $\#\,\mathrm{v}^{-1}$ | Number of juveniles per unit volume | | |
| $N_A$ | $\#\,\mathrm{v}^{-1}$ | Number of adults per unit volume | | |
| $q$ | # | Number of reproductive events | 3 | 10 |
| $r$ | # | Brood size | 1 | 11 |
| $t$ | t | Time | | |
| $\alpha$ | – | Characteristic value | | |
| $\mu_J$ | $\mathrm{t}^{-1}$ | Mortality rate for juveniles | | |
| $\mu_A$ | $\mathrm{t}^{-1}$ | Mortality rate for adults | | |
| $\nu_A$ | $\mathrm{t}^{-1}$ | Density-dependent mortality rate | | |

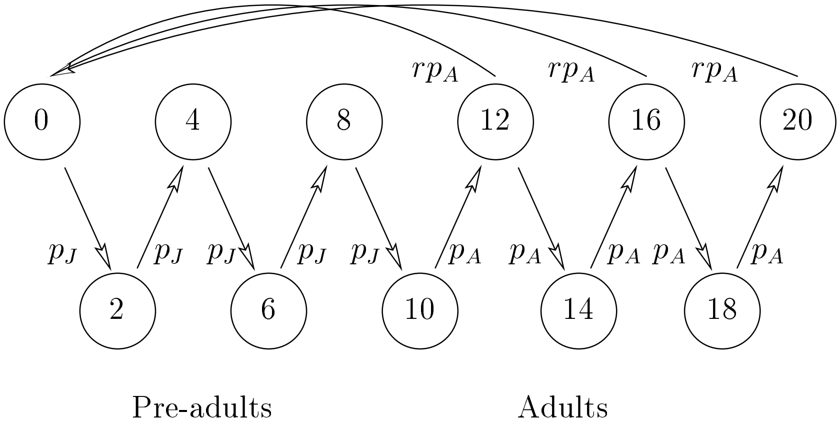

Figure 1: The life cycle graph for the population projection matrices **P**. In this example $a_A = 4$ and $a_J = 10$, so $l = 2$ and $k = 11$. The number of reproductive events is $q = 3$, thus $a_M = a_J + 3a_A = 22$. The reproductive event occur at $a = 14, 18, 22$. The survival probabilities $p_J$, $p_A$, and the fertilities $rp_A$ are indicated. The numbers are the age in the different stages.

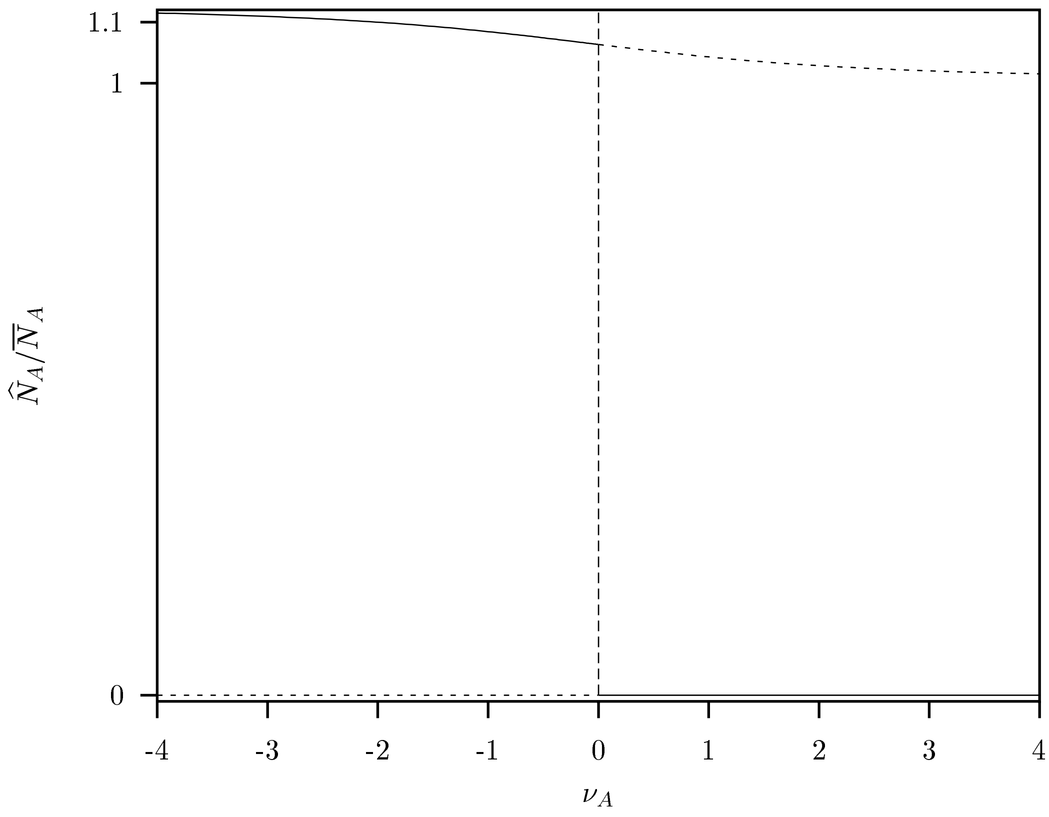

Figure 2: One-dimensional bifurcation diagram with respect to the bifurcation parameter $\nu_A$. The ratio $\widehat{N}_A/\overline{N}_A$ is plotted as function of the bifurcation parameter $\nu_A$ defined in (22). For $\nu_A < 0$ the positive steady-state is stable (solid curve) and for $\nu_A > 0$ it is unstable (dashed curve). The extinction steady-state, $\widetilde{N}_A = 0$, is unstable for $\nu_A < 0$ and stable for $\nu_A > 0$.

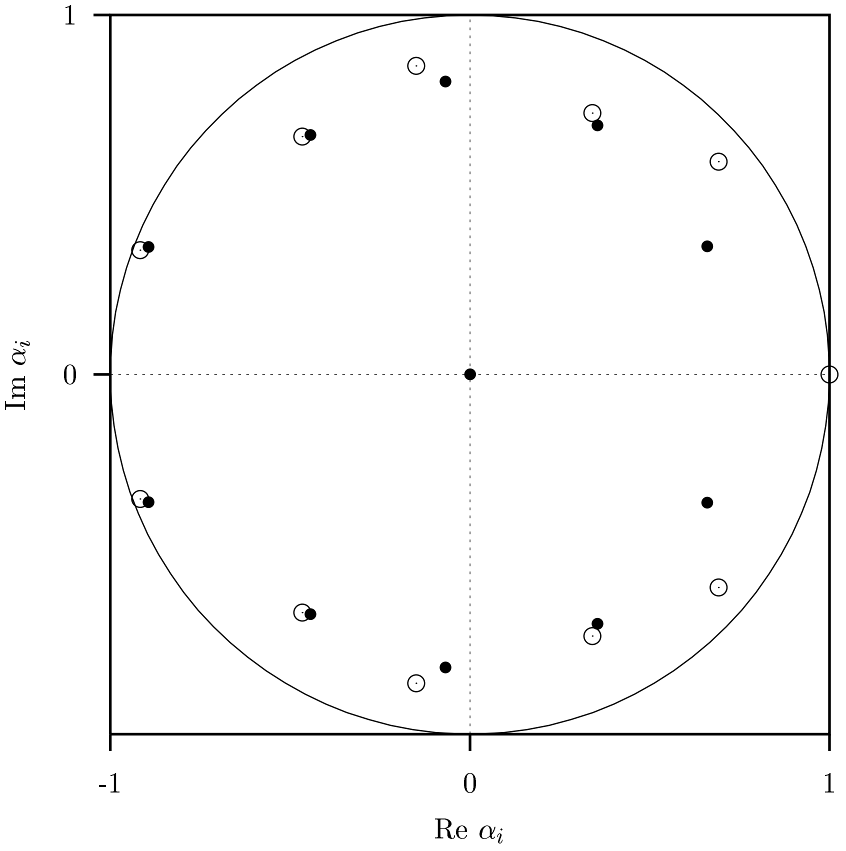

Figure 3: The eigenvalues of the linearized nonlinear system in positive steady-state for $\nu_A = 0$ (circles) and $\nu_A = -4$ (bullets) in the complex plane. The parameter settings are given in Table 1. For $\nu_A = 0$ the dominant eigenvalue is $\alpha^* = 1$. This is a bifurcation point. For $\nu_A > 0$ this dominant eigenvalue is larger than one, $\alpha^* > 1$ and this gives an unstable positive steady-state. For $\nu_A < 0$ all eigenvalues are inside the unit circle and there is stability. Notice that the real eigenvalue diminishes to almost zero for $\nu_A = -4$ but that the complex conjugate pairs change little as a function of the bifurcation parameter $\nu_A$.

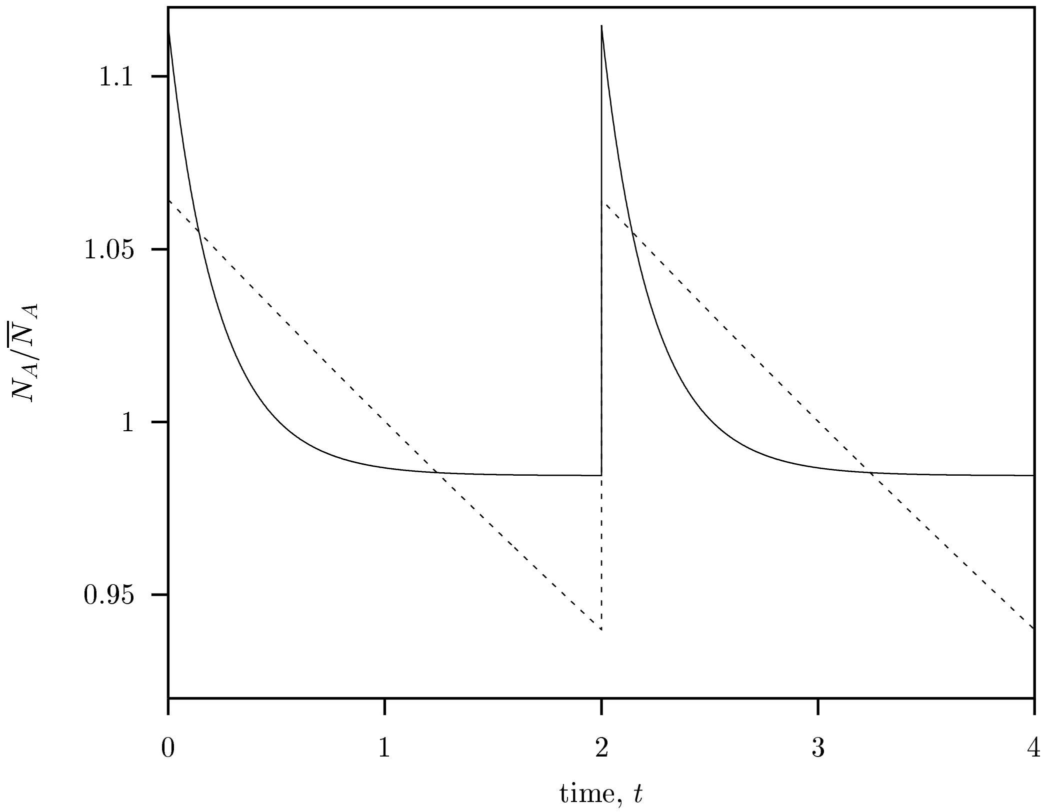

Figure 4: The number of adults $N_A(t)/\overline{N}_A$ as a function of time $t$ for $\nu_A = 0$ (dashed curve) and $\nu_A = -4$ (solid curve) for two cycles with period $T = 2$. The parameter settings are given in Table 1. With no reproduction, the asymptotic value reaches zero for $\nu_A = 0$ and for $\nu_A = -4$ $((\mu_A^* + \nu_A)\overline{N}_A)/\nu_A$, see (25). For the continuous-time formulation we have the time-invariant solution $\frac{N_A}{\overline{N}_A} = \frac{N_A^*}{\overline{N}_A} = 1$, see (22).

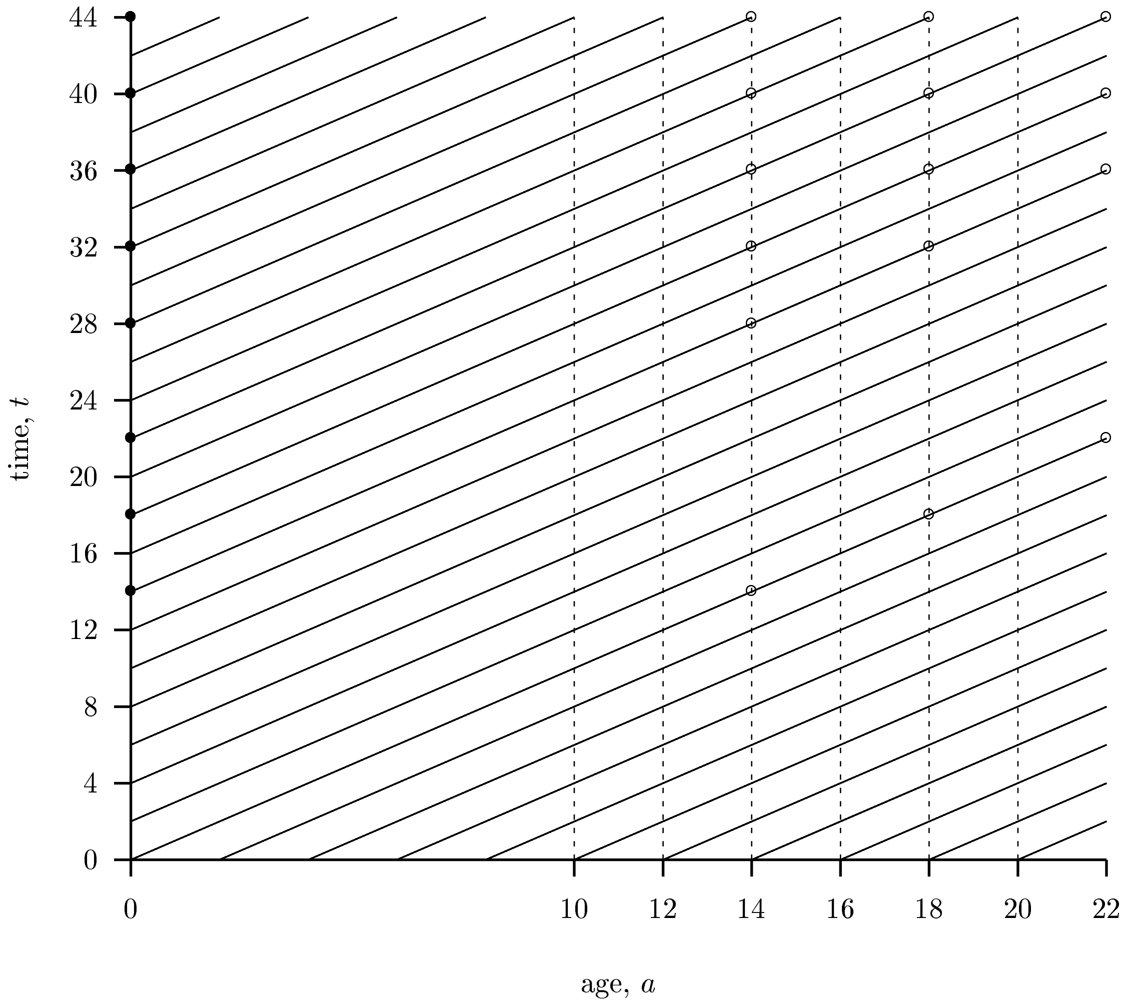

Figure 5: Cyclic solution when the ratio of $a_A$ and $a_J$ is rational. In this example $a_A = 4$ and $a_J = 10$, so $l = 2$ and $k = 11$. The number of reproductive events is $q = 3$, thus $a_M = a_J + 3a_A = 22$. The reproductive events occur at $a = 14, 18, 22$. When there is one common ancestor cohort starting with $a = 0$ and $t = 0$, the graph shows that offspring from different generations of the founder cohort is produced at the same time (circles) and they are combined into a single cohort (solid circles) leading to a finite number of cohorts. There can be only $k = 11$ different cohorts with one founder cohort.

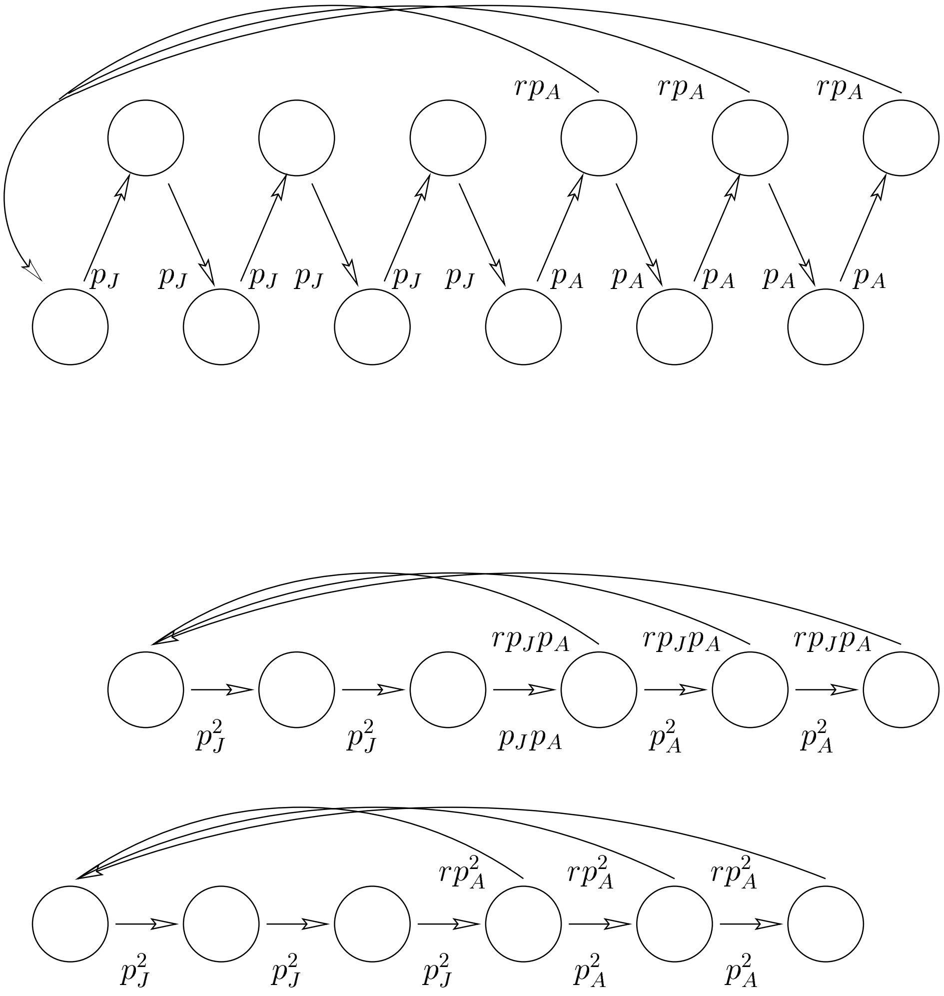

Figure 6: The life cycle graphs for the population projection matrix $\mathbf{P}$. In this example $a_A = 4$ and $a_J = 12$, but we take $l = 2$ and $k = 12$. We did not take $l = 1$ and $k = 6$ in order to have the two founder cohort case. The number of reproductive events is $q = 3$, thus $a_M = a_J + 3a_A = 24$. The reproductive events occur at $a = 16, 20, 24$. There can be only $k = 12$ different cohorts with two founder cohorts, six cohorts are descendants from one founder and six cohorts are descendants from the second founder. The two sub-graphs are disjoint, showing no mixing between the offspring of the two founder cohorts.

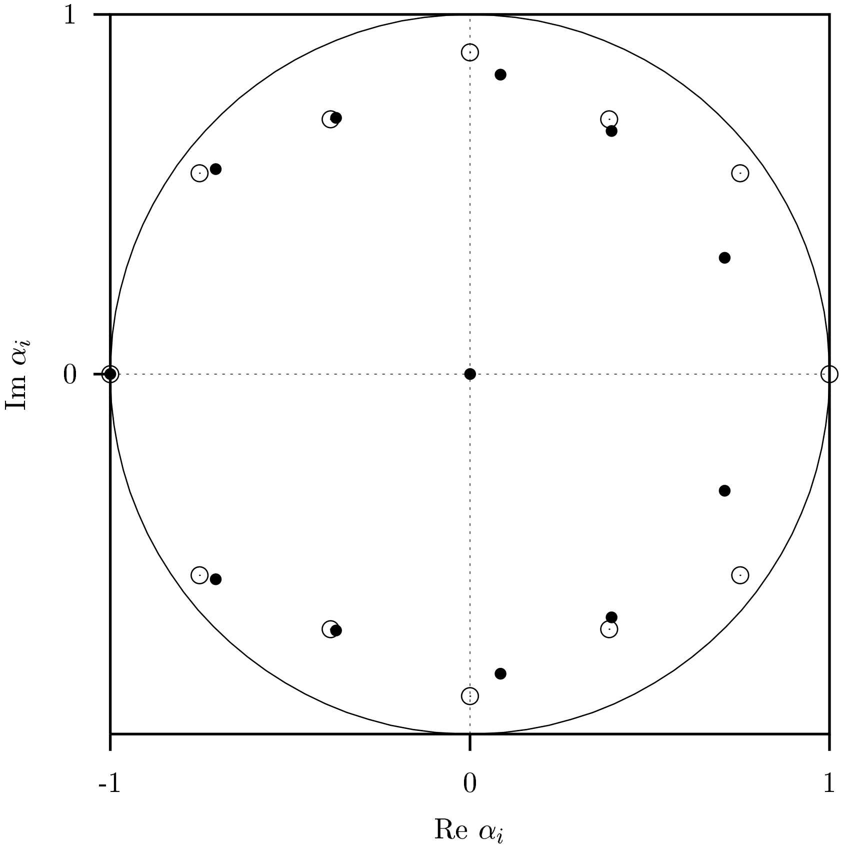

Figure 7: The eigenvalues of the linearized nonlinear system in positive steady-state for $\nu_A = 0$ (circles) and $\nu_A = -4$ (solid circles) in the complex plane, as in Figure 3. The parameters are given in Table 1 except $a_J = 12$ instead of $a_J = 10$. We took $l = 2$ and $k = 12$ and not $l = 1$ and $k = 6$ in order to have the two founder cohort case.

# PART III

# Aggregated Population Models

# 1 Introduction

Another type of model which can be used to study populations is the aggregated population model, in which all organisms grouped into one state variable are assumed to have the same defining characteristics. When studying a more complex system, i.e., one which contains a number of different species with many interactions resulting due to the structure of the food web, this approach may be a more viable option. The abstracts discussed here are extracted from manuscripts which are to be submitted for publication.

# 2 Application to Mesocosms

The aggregated model approach has been used to study the dynamics of a system, a marine mesocosm, which included phytoplankton, microzooplankton, macrozooplankton, and some higher-order consumers, such as fish, oysters, clams, and anemones [1]. The model was fine-tuned to reproduce the dynamics of the mesocosms as best as possible and then manipulated to study the effects of various scenarios on the model system. The abstract from [1] is included here:

> An energetic-based carbon flow model was developed to simulate the ecological production dynamics of 1-$m^3$ experimental marine mesocosms. The model is used to simulate mesocosm experiments that vary in ecological complexity and to investigate the effects of model structural aggregation (i.e.,

> levels of ecological detail) on predicting ecosystem response to multiple stressors. In its most detailed form, the model food web structure consists of 22 state variables that represent the primary producers and 17 that represent the consumers. The model also addresses the ecological effects of multiple stressors in the form of toxic metals and excessive nutrient levels. Primary producer biomass values are modified daily in relation to surface irradiance, water temperature, dissolved inorganic phosphorus, dissolved inorganic nitrogen, and dissolved inorganic silica values as well as through consumption by modeled grazers. Consumer biomass values change daily as a function of consumption minus energetic-based losses to respiration, excretion, locomotion, and predation. The complete model has been developed as a predictive tool for estimating ecological risks as probabilities.

The first scenario examined was the effect that three toxic metals had on the system. The following is the abstract for "Considerations of Ecological Complexity in Modeling the Impacts of Multiple Stressors on Plankton" and was work done in collaboration with S.M. Bartell, K.R. Campbell, J. Hurlebaus, J.G. Sanders and D.L. Breitburg.

> An energetics-based carbon flow model was developed to simulate the ecological impacts of arsenic (As), cadmium (Cd), and copper (Cu) on the production dynamics of a 1-$m^3$ experimental marine mesocosm. The sensitivity of predicted impacts of metals was examined in relation to three structural representations of the mesocosm food web. The most detailed model de-

> scribed the primary producers and consumers using 23 state variables. The second model used 12 and the third model used 7 state variables to represent the same mesocosm trophic structure. All three models were used to simulate the exposure of mesocosm populations to the combined metals. The results of the modeling study demonstrated that the magnitude and pattern of predicted metal impacts on plankton production depended on assumptions concerning basic model structure. The effects of model aggregation on the predicted impacts on phytoplankton production were greater than those for total microzooplankton. The results also suggested that more highly aggregated models appear to underestimate the potential impacts of metals on the plankton production.

Another study, "The Implications of Structural and Functional Food Web Heterogeneity on Modeled Marine Mesocosm Responses to Multiple Stressors" was developed in collaboration with S.M. Bartell, D.L. Breitburg and C. Richmond. The abstract follows.

> This modeling study examines the implications of imposing different degrees of structural and functional food web heterogeneity on simulated ecological impacts of nutrient enrichment and metal contamination in experimental marine mesocosms. Structural heterogeneity is defined as the number of populations used to represent different trophic guilds in food webs that describe the mesocosm. The model begins with a detailed (i.e., 39 populations

> of producers and consumers) food web used to simulate the probable impacts of multiple stressors. Successive simulations are performed with model structures that are systematically reduced in populations per trophic guild to provide simpler descriptions of the mesocosm food web (e.g., 7 populations). For each level of food web simplification, functional heterogeneity is defined by the variances assigned to the distributions of the bioenergetics parameter values that determine the production dynamics of each model population. Realistic ranges of model parameter values are developed using methods of "Monte Carlo filtering" in calibration of the models to results of mesocosm experiments. Combinations of model structural and functional food web heterogeneity are used to simulate ecological impacts and risk posed by varying exposures to nutrients (e.g., N and P) and toxic metals (As, Cd, Cu). Monte Carlo methods are implemented to develop distributions of impacts on the biomass of modeled food web populations and to identify the key model parameters that contribute to impacts and risk. The simulated impacts are compared with results measured in corresponding mesocosm experiments. The combined modeling and experimental results can be explored to develop theoretical relationships between food web complexity and food web variability on ecological responses to multiple stressors.

These are only two examples of the possibilities that can be explored with an aggregation model.

# References

# References

[1] C.M. Lovelock. An energetic-based approach to modeling ecological risks in marine mesocosms. In D. Gómez, editor, *School of Environmental Science and Technology Lectures Volume II*, pages 198–206, Buenos Aires, Argentina, 1998. Comisión Nacional de Energía Atómica.

# Vita

Cynthia M. Krohn was born in Kitchener, Waterloo, Ontario, Canada on September 12, 1972. She grew up in Tucson, Arizona and graduated from Sabino High School in 1990. In the fall of 1990, she enrolled at the University of Arizona, where she received her Bachelor of Science degree in Engineering Mathematics in the spring of 1994. In August of 1994, she began studying at the University of Tennessee in Knoxville. She received her Master of Science degree in Mathematics in the summer of 1996 and in August of 2001, she graduated with a Doctor of Philosophy degree in Mathematics.

She is currently employed by Intel Corporation in Chandler, Arizona, as a yield engineer.