Modeling the Spatio-Temporal Dynamics of Interacting Fish Species in the Northeast Continental Shelf

2018 WPI REU Program in Industrial Mathematics and Statistics

WPI REU 2018

Sara Amato, Assumption College

Lauren Moore, University of Kentucky

Katie Ragosta, Boston University

Shelby Stowe, Sterling College

Date: July 28, 2018

Approved:

Dr. Andrea Arnold, Advisor

Dr. Burt Tilley, Advisor

Abstract

Knowledge of the population dynamics of marine species is vital to understanding ocean sustain-

ability. This project aims to develop and analyze spatio-temporal single-species and multi-species

models for studying fish population dynamics in the Northeast Continental Shelf, specifically At-

lantic cod and Atlantic herring. We formulate partial differential equation models and integrodiffer-

ence models that take into account species interactions between Atlantic cod and Atlantic herring.

We determine a method to compare our single-species and multi-species models, to provide in-

formation to the Northeast Fisheries Science Center on whether either species would benefit from

being assessed with a multi-species model. All models consider species’ behavior, including sea-

sonal migrations. We employ statistical approaches such as nonlinear filtering to estimate model

parameters and quantify uncertainty in model predictions, comparing the results to synthetic data.

Acknowledgements

We would like to acknowledge the support from the National Science Foundation under grant

DMS-1757685 for the 2018 Worcester Polytechnic Institute Research Experience for Undergrad-

uates program in Industrial Mathematics and Statistics, as well as the support from the Center for

Industrial Mathematics and Statistics at WPI. We would also like to acknowledge our industrial

sponsor, the National Oceanic and Atmospheric Administration, particular the Northeast Fisheries

Science Center, as well as Dr. Sarah Gaichas for being our industrial liason. Finally, we would

like to thank the Department of Mathematical Sciences at WPI, as well as our two advisors, Dr.

Andrea Arnold and Dr. Burt Tilley.

Contents

1 Introduction 1

1.1 Motivation . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 1

1.2 DataProvided . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

1.3 FishOverview . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5

1.3.1 AtlanticHerring . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5

1.3.2 AtlanticCod . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6

2 Partial Differential Equation Models 8

2.1 Background . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 8

2.1.1 Logistic Growth Model . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9

2.1.2 Lotka-Volterra Predator-Prey Model . . . . . . . . . . . . . . . . . . . . . 9

2.2 Derivation . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 11

2.2.1 Overview . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 11

2.2.2 ConservationLawandFluxDefinition . . . . . . . . . . . . . . . . . . . . 12

2.3 Single-speciesModel . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 15

2.3.1 VelocityFunction . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 16

2.3.2 BirthRateFunction . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 18

2.4 Multi-speciesModel . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 21

2.5 NumericalMethods . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 23

i

3 Integrodifference Models 28

3.1 Background . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 28

3.2 Single-speciesModels . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 28

3.2.1 SpatialShiftFunction . . . . . . . . . . . . . . . . . . . . . . . . . . . . 30

3.2.2 Single-speciesModel . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 31

3.3 Multi-speciesModel . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 33

4 Parameter Estimation 35

4.1 Motivation . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 35

4.2 InverseProblem . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 36

4.3 EnsembleKalmanFilter . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 36

4.4 Results. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 38

4.4.1 PDE:Single-species . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 39

4.4.2 PDE:Multi-species . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 42

4.4.3 Integrodifference: Single-species . . . . . . . . . . . . . . . . . . . . . . 44

4.4.4 Integrodifference: Multi-species . . . . . . . . . . . . . . . . . . . . . . . 47

5 Model Comparison 51

5.1 ComparisonMethod . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 51

5.2 PDEComparison . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 52

5.3 IntegrodifferenceComparison . . . . . . . . . . . . . . . . . . . . . . . . . . . . 53

6 Discussion 56

6.1 Summary . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 56

6.2 InterpretationofResults . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 57

6.3 FutureWork . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 57

References 59

ii

Appendix 63

A Matlab Code 63

A.1 PartialDifferentialEquationModelCodes . . . . . . . . . . . . . . . . . . . . . . 63

A.2 IntegrodifferenceModelCodes . . . . . . . . . . . . . . . . . . . . . . . . . . . . 81

A.3 EnsembleKalmanFilterCodes . . . . . . . . . . . . . . . . . . . . . . . . . . . . 99

A.4 ModelComparisonCode . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 151

iii

Chapter 1

Introduction

1.1 Motivation

In an ever-growing world, ensuring sustainability is of the utmost concern. One industry concerned

with sustainability is the fishing industry. The Food and Agriculture Organization (FAO) of the

United Nations monitors the state of world fisheries. According to the FAO, from 1990 to 2007,

approximately one-quarter of fish stocks were overexploited, depleted, or in a state of recovering

from depletion. This accounts for 17% of fish stocks in the Northwest and Northeast Atlantic,

which is the primary area of concern in this project [1].

Historical examples demonstrate the importance of using accurate population models to ensure

that fishing is kept at a sustainable level. For instance, Atlantic cod, now classified as depleted,

were once an abundant species in the North Atlantic [2]. In 1852, the biomass of Atlantic cod

was around 1,260,000 metric tons [3]. High demand for cod combined with an underestimate of

mortality led to overfishing, and the Atlantic cod population eventually plummeted. In 2005, the

biomass of cod was estimated to be 50,000 metric tons [3].

The Northeast Fisheries Science Center (NEFSC), located in Woods Hole, MA, is a subdi-

vision of the National Oceanic and Atmospheric Administration (NOAA). The NEFSC manages

1

marine resources and provides options for balancing their harvesting and conservation. They set

restrictions on fishing and determine the target levels for fish species in the Northeast Continental

Shelf [4]. Directly observing fish abundance and behavior is difficult and expensive, therefore the

NEFSC uses mathematical models to estimate the state of fish populations [5].

Mathematical models can examine either one species or multiple species. Single-species mod-

els are simpler in comparison; however, multi-species models account for interspecies interactions.

NOAA’s National Marine Fisheries Service has many types of stock assessment models grouped

into the NOAA Fisheries Toolbox [6]. These models fall into two categories, core assessments and

research models. Core assessments are based on peer reviewed methods, while research models

have undergone testing within the organization but have not yet been subjected to peer review. Each

stock assessment model evaluates a single species. The NEFSC has also developed multi-species

models, but these are not currently used for stock assessments [7]. The NEFSC wants to ensure

their models are giving reasonable results, but they do not want to put resources into multi-species

stock assessments if the improvement in predictions is minimal.

The goal of this project is to compare single-species and multi-species models for stock assess-

ments. We aim to determine whether or not a particular species would benefit from having stock

assessments performed with a multi-species rather than a single-species model. To do this, we

begin by developing single-species and multi-species models. We develop two types of models,

partial differential equation (PDE) models and integrodifference models. We then use an ensemble

Kalman filter to estimate parameters that are poorly known due to the difficulty of observing fish

behavior. In this project, we model the Atlantic herring and Atlantic cod where the herring are

prey to the cod.

2

1.2 Data Provided

The NEFSC provided us with survey data from 1968 to 2013. Their data is collected twice every

year, once in the spring and once in the fall, from 640 different survey stations in the North-

east Continental Shelf. This region, shown in Figure 1.1, and consists of the Mid-Atlantic Bight

(MAB), Georges Bank (GB), Scotian Shelf (SS), and the Gulf of Maine (GoM). In this project, we

focus on Georges Bank.

Figure 1.1: Map of the Northeast Continental Shelf. Shelf is divided into four regions: Mid- Atlantic Bight (MAB), Geroges Bank (GB), Scotian Shelf (SS), and Gulf of Maine (GoM).

Each region is subdivided into strata. Data is collected via a bottom trawl survey (BTS) at

randomly selected strata, where each strata is an equally likely choice. In these bottom trawl

surveys, a trawling boat, shown in Figure 1.2, goes to the preselected strata, drops a net, and drags

it for 20 minutes along the ocean floor. When the time is up, the net is pulled up and the fish are

sorted by species [8]. Data is then collected for each species. This includes the abundance, or

total count, of each fish species, the total mass of the catch (in kilograms), the surface and bottom

temperature of the water (in ◦Celsius), the strata number surveyed, the latitude and longitude of the

survey location, and the region of the survey location (MAB, GB, SS, or GoM) [8]. The models in

3

Figure 1.2: Trawling boat used to conduct a BTS.

this project utilize the abundance as well as the year, season, and location of the survey.

The data within Georges Bank is shown in Figure 1.3, where each dot is a survey location. The

surveys are conducted every spring between March and May, and every fall between September

and November [8]. Since we do not know the exact month in which each survey was conducted,

we treat spring data as occurring in April and fall data as occurring in October for the purposes

of our models. Because the models in this paper are one-dimensional, the survey locations of the

two-dimensional graph are projected onto the red line, and the value at each point on the line is the

average of the abundance at each point mapped to it.

Figure 1.4 shows the abundance for Atlantic herring and Atlantic cod. Because of the noise

Figure 1.3: All survey data collected between 1980 through 2000 in Georges Bank in April and October

4

(a) (b)

Figure 1.4: The abundance of Atlantic herring (a) and Atlantic cod (b) from 1980 through 2000 in Georges Bank in April and October .level of the data, the filtering process we describe later for parameter estimation did not respond

well to the data in its raw form. We instead use synthetic data to estimate parameters, and use of

the real data is addressed further in the Future Work section of this paper.

1.3 Fish Overview

1.3.1 Atlantic Herring

Atlantic herring can grow up to 14 inches and 1.5 pounds [9]. NOAA fisheries reported that

Atlantic herring are not overfished according to the 2015 stock assessment. NOAA estimates the

Atlantic herring population is at about 517,930 metric tons, which is above their target population

of 157,000 metric tons [10].

We plot the abundance of the Atlantic herring based on the trawling data that was provided

by the NEFSC in Figure 1.5. The average abundance of the Atlantic herring in the Northeast

Continental Shelf is 8,953 fish. Herring travel in schools of up to hundreds or thousands of fish.

It is very rare to see a single herring or even a small school. Also, herring are not frightened by

5

Figure 1.5: Atlantic herring abundance on a semi-log scale over all regions in the Northeast Con- tinental Shelf.

boats, which could cause the data collected from the BTS to be skewed in comparison to other fish

species [9].

Atlantic herring do not normally prey on other fish; however, they are often preyed upon by

larger fish species [9]. Most notably, they are eaten by Atlantic cod, haddock, silver hake, striped

bass, pollock, mackerel, salmon, tuna, dogfish, and mackerel sharks [9]. Atlantic herring migrate

twice per year, north in the spring and south in the fall. The spring migration occurs between

May and June and the fall migration occurs between November and December. Spawning occurs

between July and October [11].

1.3.2 Atlantic Cod

Female Atlantic Cod can grow up to 57 inches and 54 pounds and males can grow up to 46 inches

and 43 pounds. Some Atlantic cod can grow upwards of 100 pounds [9]. NOAA fisheries re-

ported that Atlantic cod are overfished according to the 2017 stock assessment. Atlantic cod in the

Northeast continental shelf live in Georges Bank and the Gulf of Maine [2].

We plot the abundance of the Atlantic cod based on the data that was provided by the NEFSC

6

Figure 1.6: Atlantic cod abundance on a semi-log scale over all regions in the Northeast Continen- tal Shelf.

in Figure 1.6. The average abundance of the Atlantic cod in the Northeast Continental Shelf is

1,093 fish. Atlantic cod often stay close to the ocean floor, and large cod keep closer to the ground

than small ones. Atlantic cod form compact schools during the day and will scatter at night [9].

Atlantic cod consume mollusks, Atlantic herring, crabs, lobsters, shrimps, brittle stars, sea

urchins, sea cucumbers, and sea worms; there are times even a wild duck does not escape from a

large cod. Young cod, from seven to eight inches, are also eaten by the larger cod. Large sharks and

spiny dogfish sometimes prey on adult Atlantic cod [9]. Atlantic cod migrate twice per year, prior

to and after spawning [12]. They migrate north to spawning grounds in March and return south

in June [9]. Larger Atlantic cod travel very little outside of the spawning season. If they exhaust

the food supply in one spot, they are driven to move to fresh foraging grounds. Additionally, if

Atlantic cod are harassed too much by the spiny dogfish, they will move to another location [9].

7

Chapter 2

Partial Differential Equation Models

2.1 Background

For our partial differential equation (PDE) models, we consider the spatial area of Georges Bank

along the Northeast Continental Shelf. We plot the survey collection locations that were used

between 1980 and 2000 according to their specific latitude and longitude coordinates (Figure 1.1).

This gives us a two-dimensional spatial region; for simplicity, we would like our PDE model to

depend on only one spatial dimension. Therefore, we project the survey location points onto a line

to create one dimensional data.

Our PDE model takes into account advection, diffusion, and reaction. The advection term

represents a shift of the population as a whole and will take into account the migratory movements

of the Atlantic cod and Atlantic herring, that were discussed in the Introduction. Diffusion models

the spread of the population. Our reaction term will represent growth in population, as well as

interaction in the multi-species model. The reaction term uses the logistic growth equation, as well

as a variation of the Lotka-Volterra model.

8

2.1.1 Logistic Growth Model

For the logistic growth model, there are a variety of assumptions that are made for a given popu-

lation in a defined region. The first assumption is the amount of resources in the region is a fixed

amount. It is also assumed there will not be immigration or emigration from the defined region.

All individuals in the population reproduce equally, and the rate of increase in the population is

instantaneous.

The equation for the differential logistic growth model defines

dNdt = rN(1− NK), N(0) = N0 (2.1)

where r is the growth rate of the population, measured in units of reciprocal time, and K is the

carrying capacity, measured in units of number of individuals [13]. We are finding the growth of

the population N at time t.

For insight in the behavior of the population governed by (2.1), we consider two cases N1(t)

and N2(t) with the same values of r and K, but different initial conditions. We use the conditions

r = 0.1, K = 50, N1(0) = 1, and N2(0) = 60 within the differential logistic growth model and we

plot the behavior of this model (see Figure 2.1). If an initial population is chosen that is below the

carrying capacity, the population will grow until it converges at the carrying capacity. If an initial

population is chosen above the carrying capacity, the population will decrease to converge to the

carrying capacity.

2.1.2 Lotka-Volterra Predator-Prey Model

For our multi-species model, we choose to incorporate predator-prey interactions between the At-

lantic cod and Atlantic herring populations following the Lotka-Volterra model.

The growth rate of the cod is proportional to the rate of predation upon the herring, which is

represented by the term ε in (2.3) and β in (2.2) [13]. Unlike the Lotka-Volterra model, we assume

9

Figure 2.1: Differential logistic growth model where r = 0.1, K = 50, N1(0) = 1, N2(0) = 60, and time spans 100 years.

there are other prey for the cod to consume and can therefore grow in absence of the herring. We

also assume the prey population will not grow to carrying capacity in the absence of the predator

because of predation from other species.

The change in the prey population is determined by the following equation

dHdt = αH −βHC, H(0) = H0 (2.2)

where H is Atlantic herring and C is Atlantic cod. The parameters used within this model include

α, the growth rate of Atlantic herring in the absence of the Atlantic cod and is measured in units

of reciprocal time, and β, the mortality of the Atlantic herring due to predation by the Atlantic

cod is measured in units of reciprocal of the number of predators times time. The equation for the

predator population is determined by

dCdt = δβCH −γC, C(0) =C0 (2.3)

where, again, H is the population of herring and C is the population of cod. The parameter δ is

10

the growth rate of the Atlantic cod due to consumption of the Atlantic herring and is measured

in units of the number of predators divided by the number of prey. The γ term is the death rate

of the Atlantic cod in the absence of Atlantic herring and is measured in units of reciprocal time.

Figure 2.2 shows the interaction of cod and herring using the conditions α = 1, β = 0.1, δ = 0.75,

γ = 1.5, H(0) =C(0) = 20.

Figure 2.2: The values of the parameters used for this example are α = 1, β = 0.1, δ = 0.75, and γ = 1.5. The initial conditions are H(0) =C(0) = 20 and time spans 30 years. Cod popula- tions increase when herring populations are high, and high cod populations decrease the herring population. This results in the oscillations pictured.

2.2 Derivation

2.2.1 Overview

To sensibly represent a physical system, any PDE model must satisfy the conservation law which

states

∂ρ∂t +∇· φ = R(ρ, x,t) (2.4)

where we choose definitions for the flux term, φ, and the reaction term, R(ρ, x,t).

11

2.2.2 Conservation Law and Flux Definition

Flux represents movement in and out of the system, and its definition is generally based on scien-

tific observation. For our project, we define flux to be

φ = vρ −D∇ρ. (2.5)

The source term, R(ρ, x,t), represents creation and destruction within the system [14]. The source

term in our model represents population growth and population death. The reaction term in our

single species models is

R(ρ) = αρ(1− ρK)−μρ (2.6)

which is the logistic growth equation with a mortality term subtracted to account for population

decline due to fishing.

In the multi-species case, we combine the Lotka-Volterra equations for predator-prey inter-

actions with the logistic growth equation and again subtract fishing mortality terms for both the

herring and the cod. Denoting Atlantic herring with the subscript h and Atlantic cod with the

subscript c,

Rh(ρh,ρc,t) = αh(t)ρh(1− ρhKh)−βρhρc−μhρh (2.7) Rc(ρh,ρc,t) = ερhρc+αc(t)ρc(1− ρcKc)−μcρc (2.8)

where β is the predation rate of herring due to the cod and ε is the conversion efficiency rate of

cod growth due to consuming herring.

We begin by deriving the conservation law to demonstrate that the PDE must satisfy it. Con-

sider a region V and an amount of matter M inside of V. In our project, V is an arbitrary three-

dimensional region of the ocean and M is the total number of fish inside of region V. By the

12

definition of density,

M =

∫V ρ( x,t)dV (2.9)

where ρ is the mass density and has units mkg3, M is the amount of mass with units kg, and x is space.

Flux is defined as the rate at which mass flows through a given area. V is a volume. The source

term is the rate per unit volume where mass is generated or lost, notated by R(ρ, x,t). Finally, the

rate of increase of mass inV is dMdt . Mathematically, this can be written as

dMdt = dt

d∫V ρ( x,t)dV = +∫V − φ · ˆn dS+∫V F(ρ, x,t) dV (2.10)

where ˆn is the outward normal vector to V. Since V is independent of time, equation (2.10) can be

simplified to

dMdt =

∂ρ∂t dV = −∫∫∫φ · ˆn dS+F dV. (2.11)

V V V From here, the Divergence Theorem is applied. The theorem states that given a differentiable

vector field φ on a volume V: ∫φ · ˆn dS =

dV ∫V ∇· φ dV. (2.12)

Figure 2.3: A control volume V through which a flux φ of fish flows.

13

From (2.11), we find that ∫V

∂ρ∂t +∇· φ −F(ρ, x,t) dV = 0. (2.13)

∂ρ∂t +∇· φ = F(ρ, x,t). (2.14)

Applying (2.13) to the φ term in equation (2.11) yields

∫∂V φ · ˆn dS =

∫V ∇· φ dV. (2.15)

Then, since all three terms are integrated with respect to V, we can condense

∫V

dρdt dV = −∫∂V φ · ˆn dS+∫V R dV (2.16)

to ∫V

(∂ρ∂t +∇· φ −R(ρ, x,t))

dV = 0. (2.17)

dV = 0. (2.17)

Since V is an arbitrary volume, then the integrand of (2.17) must be identically zero, so

∂ρ∂t = −∇· φ +R(ρ, x,t), (2.18)

where

φ = vρ −D∇ρ. (2.19)

Since divergence is a linear operator,∇· φ = ∇·( vρ)−∇·(D∇ρ). (2.20)

14

With the addition of a reaction term R(ρ, x,t), the conservation law gives the general form

∂ρ∂t = −∇·( vρ)+∇·(D∇ρ)+R(ρ, x,t). (2.21)

The PDE in this paper will only examine one spatial dimension, so (2.21) can be simplified for

spatially uniform D to

∂ρ∂t = − ∂∂x(vρ)+D∂2ρ

∂x2 +R(ρ,t). (2.22)

In the next section, we will further describe the terms in 2.22, including the velocity term and the

reaction term.

2.3 Single-species Model

For our single-species models, we account for the seasonal migrations and spawning seasons of

the Atlantic cod and the Atlantic herring. Recall, the Atlantic cod spawn annually April through

May, and Atlantic herring spawn annually July through October [11]. Atlantic cod generally stay

in the same area, called their home range, throughout the year, but they do migrate to spawn. Their

spring migration occurs in March, and they migrate back to their home range in June [9].

For the general PDE single-species model, we construct an advection-diffusion-reaction equa-

tion

∂ρi ∂t = −vi(t)∂ρi

∂x +Di∂2ρi

∂x2 +Ri(ρi,t) (2.23)

where the subscript i represents the species being modeled, i = h for Atlantic herring and i = c

for Atlantic cod, and ρi is the population density of the species. The advection term is dependent

on velocity, vi(t), which models the migration movement for the species. The diffusion term is

dependent on the diffusion coefficient, Di, which models the spatial spread of the species. The

15

reaction term, Ri(ρi,t), is defined as

Ri(ρi,t) = αi(t)ρi(1− ρiKi)−μiρi. (2.24)

The reaction term models the population dynamics of the species. αi(t) represents the population

birth rate, Ki represents the carrying capacity, and μi is the death rate of the population.

We describe our modeling choices for vi(t) and αi(t) in the following subsections. Since exact

analytical solutions to these families of PDE’s are not known, the choices for vi(t) and αi(t) need

to be amenable to computational simulation of these equations. Hence, we are going to require

smooth, continuous functions to represent these different fish behaviors.

2.3.1 Velocity Function

The migratory movements of the Atlantic cod and the Atlantic herring are dependent upon time

of year, therefore we create respective velocity terms dependent on time to model this spatial

movement. Both species migrate to spawning grounds once every year. In order to represent these

migration patterns, the velocity function is zero during most of the year when there is no migration,

positive during spring migration, and negative during fall migration.

We construct a piecewise function using hyperbolic tangent functions (see Figure 2.27 and

Figure 2.29). The general form of the tanh function is

f(t −t0) = a2[c+tanh(b[t −t0])] (2.25)

where a determines if the function is multiplied by one or negative one, in other words whether the

step approximated by the function is a step up or a step down. The b term determines the steepness

of the function. In this paper, b = 200 in all cases to model the change between moving and not

moving. The c term determines the vertical shift of the function, c = 1 for the functions shaping

16

the positive pulse and c = −1 for the negative pulse. The horizontal shift, t0, gives the location of

the midpoint of the step.

For the Atlantic herring, we change the values of a, c, and t0 depending on the time of year to

match their migratory patterns to create

vh(t) = a2[c+tanh(200[t −t0])] (2.26)

where a a = = −1,c 1,c = = −1,t1,t0 0 = = 12 212 30 ≤t ≤ 12 5512 < t ≤ 912 a a = = −1,c 1,c = = −1,t1,t0 0 = = 12 12 56912 < t ≤ 1112 1112 < t ≤ 1

. (2.27)

For the Atlantic cod, we change the values of a, c, and t0 depending on the time of year to

Figure 2.4: Atlantic herring velocity for the PDE model shows that from January to May and from June to November the Atlantic herring do not migrate because vh = 0. From May to June the Atlantic herring migrate north because vh = 1. From November to December the Atlantic herring migrate south because vh = −1. The migration pattern will repeat for each additional year.

17

follow the species migratory pattern and construct their velocity term to be

vc(t) = a2[c+tanh(200[t −t0])] (2.28)

where a a = = −1,c 1,c = = −1,t1,t0 0 = = 12 212 30 ≤ t ≤ 2.512 2.512 < t ≤ 412 a a = = −1,c 1,c = = −1,x1,t0 0 = = 12 512 612 4<t ≤ 5.512 5.512 < t ≤ 1

(2.29)

Figure 2.5: Atlantic cod velocity for the PDE model shows that from January to March, May to June, and July to December the Atlantic cod do not migrate because vh = 0. From March to May the Atlantic cod migrate north because vh = 1. From June to the July the Atlantic cod migrate south because vh = −1. The migration pattern will repeat for each additional year.

2.3.2 Birth Rate Function

We use birth rate functions for Atlantic cod and Atlantic herring to model their spawning as de-

pendent on time. Both Atlantic herring and Atlantic cod spawn annually: the herring from July to

October and the cod from April to May. To represent this, the birth rate function α(t) should be

zero during most of the year and positive only during the spawning season.

18

For the birth rate function, we use a Gaussian distribution such that

α(t) = √2πσ1 2e

−(t− 2σ ̄μ)2 2

(2.30)

(2.30)

where the midpoint of each spawning season is the mean, ̄μ, and the standard deviation, σ, rep-

resents the duration of the spawning season. This allows the birth rate to be zero for most of the

year and for the majority of the spawning season to occur at the midpoint of each spawning season.

A larger σ represents a longer spawning season. The midpoint for the Atlantic herring spawning

season is the beginning of September, therefore ̄μ = 712. The Atlantic herring have a spawning

season that lasts four months, so σ will be larger for the Atlantic herring. The midpoint for the

Atlantic cod spawning season is the beginning of May, therefore ̄μ = 125. The Atlantic cod have a

spawning season that lasts two months, so σ will be smaller for the Atlantic cod. The Atlantic cod

produce less offspring than the Atlantic herring, so the magnitude of the birth rate is smaller (see

Figure 2.6).

Figure 2.6: The Atlantic herring birth rate for the PDE models and integrodifference models where ̄μ = 712 and σ = 0.035. The Atlantic cod birth rate for the PDE models and integrodifference models where ̄μ = 512 and σ = 0.025.

19

The general single-species model for Atlantic herring and Atlantic cod is as follows:

∂ρi ∂t = −vi(t)∂ρ∂x i

+Di∂2ρi

∂x2 +Ri(ρi,t) (2.31)

Ri(ρi,t) = αi(t)ρi(1− ρiKi)−μiρi. (2.32)

The initial conditions are chosen to be:

ρh(x,0) = 5(x(3−x))6 √12π e

−(x)2 2

+10 (2.33)

ρc(x,0)=(x(3−x))6 √12πe

−(x)2 2

+10. (2.34)

Using the parameters in Table 2.1, we graph the solution to the model for Atlantic herring and

the Atlantic cod. The parameters were chosen in order to show the interaction of the different

functions in the model.

In Figure 2.7, the Atlantic herring begin to slowly decrease in population. The spawning sea-

sons are represented by the increases and decreases of the population. The population increases

during the spawning season and will decrease when no new fish are born. The migration patterns

are also seen in Figure 2.7.

In Figure 2.8, you can see the Atlantic cod begin to slowly decrease in population. The spawn-

ing seasons are represented by the increases and decreases of the population. The population

increases during the spawning season and will decrease when no new fish are born. Note the mag-

Meaning Parameter Herring Value Cod Value Carrying capacity Ki 100 50 Mortality rate μi 0.5 1.5 Diffusion constant Di 0.1 0.005

Table 2.1: Parameters for single-species PDE models to show the interaction of the different func- tions vi(t) and αi(t).

20

Figure 2.7: Results of the evolution of the single-species PDE model (2.31) using the initial con- ditions (2.33) for the parameter values are shown in Table 2.1.

Figure 2.8: Results of the evolution of the single-species PDE model (2.31) using the initial con- ditions (2.34) for the parameter values are shown in Table 2.1.

nitude of the Atlantic cod is smaller than the Atlantic herring. This is because there are fewer

Atlantic cod than there are Atlantic herring as defined in Table 2.1. In Figure 2.8, you can see the

movement of the Atlantic cod, which is from the migration.

2.4 Multi-species Model

We examine the relationship between the Atlantic cod and the Atlantic herring. Recall the Atlantic

cod is the predator in the relationship, and the Atlantic herring is the prey. The following coupled

model displays the interaction between the pair using the same components of the single-species

21

models, but additionally uses a Lotka-Volterra type interaction. The coupled model is as follows:

∂ρh ∂t = −vh(t)∂ρh

∂x +Dh∂2ρh

∂x2 +Rh(ρh,ρc,t) (2.35)

∂ρc ∂t = −vc(t)∂ρc

∂x +Dc∂2ρc

∂x2 +Rc(ρh,ρc,t) (2.36)

where,

Rh(ρh,ρc,t) = αh(t)ρh(1− ρhKh)−βρhρc−μhρh (2.37) Rc(ρh,ρc,t) = ερhρc+αc(t)ρc(1− ρcKc)−μcρc (2.38)

are the growth rate functions. These growth rate functions show the predator-prey relationship

between the Atlantic cod and the Atlantic herring. Observe, the logistic growth function. Note,

βρhρc is being subtracted from the logistic growth portion in the Atlantic herring portion of the

multi-species model, which accounts for the mortality of Atlantic herring due to being consumed

by the Atlantic cod. In the Atlantic cod part of the multi-species model, ερhρc is being added to

the logistic growth part. This is the conversion efficiency, which accounts for the growth rate of the

Atlantic cod from consuming the Atlantic herring. The velocity and birth rate functions for each

species are unchanged from the single-species model.

Using the parameters in Table 2.1, we graph the solution to the multi-species model for Atlantic

herring and Atlantic cod. Additionally, the initial conditions for the PDE multi-species model

match the single-species initial conditions defined in (2.33) and (2.34).

In Figure 2.9 the Atlantic herring and the Atlantic cod populations start out at their initial

conditions. We can see an initial growth in the cod population and an initial decrease in the herring

population. We can also see that cod growth follows increases in the herring population.

22

Figure 2.9: Results of the evolution of the multi-species PDE model (2.35) and (2.36) using the initial conditions (2.34) and (2.33) for Atlantic Herring and Atlantic Cod. Parameter values are shown in Table 2.1.

2.5 Numerical Methods

Since analytical solutions to the system (see (2.35) and (2.36)) are not evident, we are required to

use computational techniques to find approximate solutions to these equations. For simplicity, we

adopt the notation

ρ(xj,tn) ≈Unj . (2.39)

Where U is the solution matrix approximating the population density function at points xj and tn [15]. Let ∆x = h and ∆t = k For ∂ρ∂t , we use a forward difference in time

∂ρ∂t ≈ Un+1 j −Unj

k . (2.40)

For the advection term, we use the upwinding method. We start by using a one-sided approximation

to ∂ρ∂x,

∂ρ∂t ≈ −vUnj −Unj−1

h . (2.41)

23

We combine this with a forward difference in time, as shown in (2.41), and apply the approxima-

tions to the advection equation,

∂ρ∂t = −v∂ρ∂x (2.42)

to find the upwinding method

Un+1 j =Unj − vkh

(Unj −Unj−1), (2.43)

which is first order accurate in both space and time [15].

For the diffusion term, we use the Crank-Nicolson method, which approximates a solution to

the diffusion equation

∂ρ∂t = D∂∂x2ρ

2 (2.44)

by approximating ∂ρ∂t using a forward difference in time and ∂ 2ρ

∂x2 using the average of two central difference approximations at times t and t +1

∂2ρ ∂x2 ≈ DUj−1 n+1 −2Uj n+1 +Uj+1 n+1 2h+U2 nj−1−2Unj +Uj+1

n. (2.45)

For the reaction terms, we replace ρ(xj,tn) with Unj . This is referred to as the forward Euler

method, and it is the first order case of the Adams-Bashforth family of explicit approximations [15].

Using the upwinding, Crank-Nicolson, and forward Euler methods, we rewrite Equation (2.22) as

−Un+1 j −Uj

nk = (Uj n−Uh nj−1)

+ (Unj−1−2Unj h2 +Unj+1)

+R(Unj ), (2.46)

and we rearrange so the n+1 terms are on the left-hand side and the n terms are on the right-hand

24

side

− h12Un+1 j−1 +(1+ h22)Uj n+1 − h12Un+1 j+1 =Unj + hk(Unj −Unj−1)+ hk2(Unj−1−2Unj +Unj+1)+kR(Unj ). (2.47)

The left-hand side of (2.47) can be written as

(I− h12B)Un+1 (2.48)

and the right-hand side becomes(I+ hkA+D hk2B)Un+kR(Un) (2.49)

where

A =

−1 0 0 0 ... 0 1 −1 0 0 ... 0

0 1 −1 0 ... 0 ... ... ... ... ... ...

0 0 ... 0 1 −1

0 0 ... 0 0 1 

(2.50)

B =

−2 1 0 0 ... 1 0 0 ... −2 1 0 ... 1 −2 1 ... ... ... ... ... 0 ... 1 −2 0 0

0 ...

1  0 0 ... 0 1 −2(2.51)

and

25



. (2.52)

We enforce the zero-slope boundary conditions through the use of image points, which results

in the modified matrices for A and B respectively

A =

U1nU2nUn = ...

Um−1 nUm n0 1 0 0 ... 0 −1 1 ... 0 0 0 ... 0 0 0 ... 0

−1 0 ... 0 ... ... ... ...

... 0 1 −1

0 0 ... 0 0 0 

(2.53)

and

B =

−2 1 0 0 ... 2 0 0 ... −2 1 0 ... 1 −2 1 ... ... ... ... ... 0 ... 1 −2 0 0

0 ...

1 0 0 ... 0 2 −2. (2.54)

We can then write (2.47)

Un+1 =

(I− h12B)−1[(I+ hkA+D hk2B)Un+kR(Un)]. (2.55)

To resolve stability issues during the first time step of the model, we use bootstrapping. Instead of

26

computing the first time step directly, we define a smaller time step

k2 = k22 (2.56)

and evaluate the model with a time step of k2 until we reach t = k. We save the model output

at time t = k as the value of our first update, and then we return to updating with a time step of

k. Smaller time steps allow the model to make more accurate approximations of the solution, but

running the model with a very small time step for the total time period would require much more

computational power than using a larger time step. To make the model more stable but maintain

efficiency, we use this smaller time step, k2, only at the beginning of our time period to better

capture initial behavior without sacrificing computational time.

27

Chapter 3

Integrodifference Models

3.1 Background

Integrodifference models are commonly used for ecology applications such as invasive species

models [16]. The integrodifference model gives a total population. Our model is comprised of two

parts, a survival rate and a net growth rate. The net growth rate includes a kernel and a growth

term [17]. There are a variety of possibilities for the growth term; for our project, we use the

differential logistic growth equation to mirror the PDE models. Also, there are different options

for the kernel; we use the Gaussian kernel. Additionally, we use the trapezoidal rule to numerically

approximate the definite integrals in the integrodifference models

3.2 Single-species Models

The general form of our integrodifference model is

Ni, t+1(x) = s Ni, t(x−vi(t)) +∫ ba

[]k(x−y) f(Ni, t(y))dy, (3.1)

28

where

f(Ni, t(y)) (= αi(t)Ni, t(y)1− Ni, t(y)

Ki

)

(3.2)

and

s = e−μi∆t. (3.3)

We let i represent either Atlantic herring, h, or Atlantic cod, c. In our model, we measure time t

as months. The output of this model, Ni, t+1(x), is the net population of the species at location x

and time t +1. Each term in this model contributes to the net population. First, s is the probability

of survival at location x and time t and Ni, t(x−vi(t)) is the population at location x and time t.

These two terms multiplied together, sNi, t(x−vi(t)), yield the total amount of the population that

survived from time t and location x. The integral represents the net population growth at time t.

The transition kernel, k(x−y)dy, represents the probability that two individuals are separated by a

distance of (x−y) units. The population growth function, f(Ni, t(y)), is the population growth at

location y and time t. Therefore, adding the net population that survived at location x and time t to

the population growth yields the population at time t +1 and location x [16].

In our models, e−μi∆t is the probability of survival at location x and time t. Also, k(x−y)dy is

the Gaussian kernel of the formk(x−y)dy = √2πσ1 2 e− (x−y− 2σ2 ̄μ)2

dy, (3.4)

where ̄μ = 0 and σ = 2. For the growth term, we use f(Ni, t(y)), which is the differential logistic

growth equation. In the logistic growth equation, αi(t) represents the growth rate, and we use

equation 2.30. The term Ni, t(x−vi(t)) is the population at time t shifted by vi(t), where vi(t) is

the velocity function, which is determined by the migration pattern of each species. We describe

the velocity function in more detail in the following section.

29

3.2.1 Spatial Shift Function

The spatial shift vi(t) appears in the term Ni, t(x−vi(t)). This is the population at time t and space

x−vi(t). Shifting by vi(t) accounts for migration. The whole population of Atlantic herring or

Atlantic cod in space x will shift either north or south depending on the season. Recall, from the

Introduction, that Atlantic cod migrate north in March and south in June. The Atlantic herring mi-

grate north from May to June and south from November to December. To represent this, the spatial

shift, vi(t), should be zero during most of the year, positive during spring migration, and negative

during fall migration. The spatial shift function for the integrodifference model is similar in shape

to the velocity function used in the PDE model; however, here we use a Heaviside function. This

was chosen over the hyperbolic tangent function because we do not need the graph to be smooth

or continuous.

Figure 3.1: These are the spatial shift functions for the Atlantic cod and the Atlantic herring for the integrodifference model. When vi(t) = 1, Ni, t(x−vi(t)) represents the population at time t shifted north of x. Similarly when vi(t) = −1, Ni, t(x−vi(t)) represents the population at time t shifted south of x. When vi(t) = 0, no shift occurs.

30

3.2.2 Single-species Model

The initial populations are chosen to be:

Nh,0(x) = 4(x(3−x))6 √12πe

−(x)2 2

+10 (3.5)

+10 (3.5)

Nc,0(x) = 2.5(x(3−x))6 √12πe

−(x)2 2

+10. (3.6)

+10. (3.6)

Figure 3.2 and Figure 3.3 show the model output for Atlantic herring and Atlantic cod using the

parameters in Table 3.1. As an example, we selected parameters that clearly show the interaction

of the different terms in the model.

Parameter Meaning Herring Value Cod Value μi Mortality rate 0.5 0.2 αi Growth rate scale 5 2 vi Velocity magnitude 1 1 Ki Carrying capacity 100 50 ∆t Time step 1112 12 Table 3.1: Parameters for single-species Integrodifference models to show the interaction of the different functions vi(t) and αi(t)..

Figure 3.2: This figure shows the populations at each time and space step using (3.1). The initial conditions are (3.5) and the parameters are stated in Table 3.1.

31

Figure 3.2, shows the growth of the Atlantic herring population over 15 years. Additionally,

in Figure 3.2 you can see increases and decreases in the Atlantic herring population. This is due

to the Atlantic herring’s population growing during spawning season and then decreasing when

there is no spawning. The shift caused by the velocity function is seen in the changes in population

along the x-axis.

Figure 3.3 shows the growth of the Atlantic cod over the same 15 years. Because the initial

population is larger than the carrying capacity, the population declines. Over time, the population

begins to recover. The magnitude of the Atlantic cod in Figure 3.3 is smaller than the magnitude

of the Atlantic herring in Figure 3.2. This is because there are more Atlantic herring than Atlantic

cod in the ocean. Additionally, in Figure 3.3 you can see increases and decreases in the Atlantic

cod population. This is due to the Atlantic cod’s population increasing during spawning season

and decreasing during the rest of the year. The shift caused by the velocity function is seen in the

changes in population along the x-axis.

Figure 3.3: This figure shows the populations at each time and space step using (3.1). The initial conditions are (3.6) and the parameters are stated in Table 3.1.

32

3.3 Multi-species Model

Now, we examine the relationship between the Atlantic cod and the Atlantic herring. Recall that the

Atlantic cod is preys on the Atlantic herring. The following coupled model displays the interaction

between the pair using the same components as the single-species models, but it also uses a Lotka-

Volterra type interaction. The coupled model is as follows:

Nh, t+1(x) = e−μh∆t Nh, t(x−vh(t)) +∫ []k(x−y) f(Nh, t(y))dy (3.7)

Nc, t+1(x) = e−μc∆t Nc, t(x−vc(t)) +∫ []k(x−y) f(Nc, t(y))dy, (3.8)

where the growth rate functions

f(Nh t(y)) = αhNh, t(y))(1− Nh, Kt(y)

h

)−βNh, t(y)Nc,t(y) (3.9)

f(Nc, t(y)) = αcNc, t(y)(1− Nc, Kc

t(y)

)+εNh, t(y)Nc, t(y) (3.10)

show the predator-prey relationship between Atlantic cod and Atlantic herring. Observe that in

(3.9), βNh, t(y)Nc, t(y) is being subtracted from the logistic growth term. This accounts for the mor-

tality rate of Atlantic herring due to being consumed by the Atlantic cod. In (3.10), εNh, t(y)Ni, t(y)

is being added to the logistic growth term. This accounts for the growth rate of the Atlantic cod

from consuming the Atlantic herring.

The initial conditions for the multi-species model are:

Nh,0(x)=(x(3−x))6 √12πe

−(x)2 2

+10 (3.11)

Nc,0(x) = 0.25(x(3−x))6 √12πe

−(x)2 2

+10. (3.12)

33

Using the parameters in Table 3.2, we graph the solution to the multi-species model for Atlantic

herring and Atlantic cod. The length of time is increased from 15 years to 50 years to show the

predator-prey interaction over a longer period of time.

Parameter Meaning Herring Value Cod Value μi Mortality rate 1.5 0.5 αi Growth rate scale 0.5 0.5 vi Velocity magnitude 1 1 Ki Carrying capacity 150 25 ∆t Time step 112 112 Table 3.2: Parameters for multi-species integrodifference models using (3.7) and (3.8) to show the interaction of the different functions vi(t) and αi(t)..

Figure 3.4: Results of the multi-species model (3.7) and (3.8) using the initial conditions (3.11) and (3.12) for Atlantic Herring, and Atlantic Cod respectively. Parameter values are shown in Table 3.2.The Atlantic cod population spikes due to the abundance of the Atlantic herring at the beginning

of Figure 3.4. This causes a decrease in the Atlantic herring population, and the Atlantic cod

population eventually decreases because there are fewer Atlantic herring. This allows for the

Atlantic herring population to recover. Soon after, the Atlantic cod population increases because

there are more Atlantic herring to consume. This relationship continues over time.

34

Chapter 4

Parameter Estimation

4.1 Motivation

All of our models rely on parameters based on the behavior of the Atlantic cod and the Atlantic

herring. However, many of these behaviors have not been quantified from direct observation,

therefore their real values are unknown. In order to get reasonable estimates for these unknown

parameters, we use an ensemble Kalman filter. Within our models, there are five parameters we

chose estimate. For the single-species PDE Atlantic herring model and Atlantic cod model, we

estimate the carrying capacities and the diffusion coefficients. For the multi-species PDE model,

we estimate the carrying capacities, diffusion coefficients, rate of predation on herring by cod, and

conversion efficiency. For the single-species integrodifference models, we estimate the carrying

capacities and the death rates. For the multi-species integrodifference, we estimate the carrying

capacities, death rates, predation rate, and conversion efficiency.

35

4.2 Inverse Problem

Determining unknown parameters that fits a given model and system is considered an inverse

problem. Solving inverse problems requires a known model function and discrete observations of

the system being modeled, but the parameters and initial states may be unknown or poorly known.

There are many ways to approach solving inverse problems [18]. We solve for our unknown

parameters using the Bayesian perspective. This allows for states and parameters to be treated as

random variables with probability distributions. We understand our solution, also called our joint

posterior density, to be

π(x,θ | y) ∝ π(y | x,θ)π(x,θ) (4.1)

which says the probability of our states and parameters given our observations, is proportional to

the probability of our observations given our states and parameters multiplied by the probability of

our states and our parameters [19].

4.3 Ensemble Kalman Filter

We use a parameter estimation algorithm known as the ensemble Kalman filter to estimate the

parameters in our models. In particular, the augmented ensemble Kalman filter allows for the un-

known model states and parameters to be estimated simultaneously. It utilizes our model’s outputs

as well as observation data to determine a best estimate for parameter values. An ensemble Kalman

filter approaches the inverse problem from the Bayesian perspective, meaning we will treat states

and parameters as random variables with probability distributions. Each probability distribution is

represented by random samples known as ensemble members. At each time step within the filter,

the random samples are updated and we calculate their means and standard deviations. The final

mean is our resulting parameter estimate [19].

The ensemble Kalman filter algorithm is comprised of two steps: a prediction step and an

36

analysis step. For the prediction step, we begin by assuming the current density, represented in

terms of N ensemble members, is

Sj|j = (x1j|j,θ1j ),(x2j|j,θ2j ),...,(xNj|j,θNj ) (4.2)

where x represents states and θ represents parameters. Each state prediction ensemble is updated

at every time step following the equation

xnj+1|j = F(xnj|j,θj n)+vnj, n = 1,2,...,N (4.3)

where F is a known model function and vnj is added noise, accounting for error in the model

prediction. Next in the prediction step, we create an augmented vector, z, of states and parameters

such that

znj+1|j =

xnj+1|j θnj

, n = 1,2,...,N. (4.4)

Then, we compute the ensemble statistics which include the mean,

̄zj+1|j = N

1n=1∑Nznj+1|j (4.5)

and the prior covariance matrix,

Γj+1|j = N −1

1

∑N(znj+1|j − ̄zj+1|j)(znj+1|j − ̄zj+1|j)T. n=1(4.6)

Next, we begin the analysis step. For the analysis step we utilize observation data, yj, to create

an observation ensemble

ynj+1 = yj+1+wnj+1, n = 1,2,...,N (4.7)

37

where observation error, wnj+1, is added to each ensemble member. Once we have our observation

ensemble, we compute the observation prediction ensemble

ˆynj+1 = g(xnj+1|j,θnj ), n = 1,2,...,N (4.8)

where g is the nonlinear observation model. We also need to compute the Kalman gain for every

time step in the filter

Kj+1 = σzˆyj+1(σ ˆyˆyj+1+σyj+1)−1 (4.9)

where σzˆyj+1 is the cross covariance of the state and observation predictions, σ ˆyˆyj+1 is the forecast error covariance of the observation prediction ensemble, and σyj+1 is the observation noise covari-

ance.Once these have been computed, we can calculate our posterior ensemble

znj+1|j+1 = znj+1|j +Kj+1(ynj+1− ˆynj+1), n = 1,2,...,N (4.10)

and posterior ensemble statistics, the means and covariances, for every state and parameter in-

cluded in our ensemble members. In the final time step, the calculated means of the parameters are

the parameter estimates.

4.4 Results

We are doing validation of our parameter estimation using synthetic data generated from our mod-

els, allowing us to begin with data that has more predictable behavior. To generate synthetic data,

we add noise that follows a Gaussian distribution to our model’s output. The Gaussian distribution

is predetermined with a chosen variance and mean. In order to mimic the real NEFSC data pro-

vided, our synthetic data has values correlating to data being collected twice per year, in April and

38

October, as in the NEFSC’s spring and fall data surveys. After validating the filter with synthetic

data, we hope in the future to utilize the real data to estimate chosen parameters.

4.4.1 PDE: Single-species

For our partial differential equation single-species models, we estimate the carrying capacities of

Atlantic cod and Atlantic herring, Kc and Kh, as well as their diffusion coefficients, Dc and Dh,

respectively. The first step in the parameter estimation process is to run our model with selected

parameter values to determine the true solution of the model. To find our true solutions, we run

our models using the parameter values found in Table 4.1. First, we estimate our carrying capacity

and diffusion coefficient for the single-species Atlantic cod PDE.

Meaning Parameter Herring Value Cod Value Mortality rate μi 0.5 0.01 Growth rate scale αi 3 1 Velocity magnitude vi 1 1

Carrying capacity Ki 100 20 Diffusion coefficient Di 0.1 0.1

Table 4.1: Parameter values used in computing single-species PDE model solutions, where esti- mated parameters are highlighted in red.

Parameter True Value Estimated Value Relative Error Kc 20 19.0627 0.0469 Dc 0.1 0.0314 0.686

Table 4.2: Relative error for Atlantic cod single-species PDE estimated parameters.

When we run our ensemble Kalman filter, we take the means of all of our ensemble members

and plot these over the time span of 15 years. As seen in Figure 4.1, the Atlantic cod ensemble

mean follows the same pattern as the true solution, which confirms that our filter is doing what

it is supposed to. Turning to Table 4.2 and Figure 4.1 we see that our filter estimates the true

39

Figure 4.1: The true solution and the estimated mean of the filter ensembles of the single-species model, using (2.31) and the initial conditions (2.34) for Atlantic cod. This figure also shows the ensemble Kalman filter’s estimate for Kh and Dh. The black line represents the true solution of the parameter. The solid red line represents the estimated value of the parameter over time. The dotted red lines are two standard deviations of error about the estimated parameter. The true and estimated parameter values are shown in Table 4.2.

value of the carrying capacity, 20 as 19.0627. This gives a relative error of 0.0469. Similarly, for

the diffusion coefficient, the filter estimates the real diffusion coefficient of 0.1 to be 0.0314 with a

relative error of 0.686. The estimated parameters for carrying capacity and the diffusive coefficient

are an underestimate of the true parameters.

Next, we estimate our carrying capacity and diffusion coefficient for the single-species Atlantic

herring PDE. In Figure 4.2, the Atlantic herring ensemble mean follows the same pattern as the true

solution, which confirms that our filter is doing what it is supposed to. Turning to carrying capacity

in Table 4.3 and Figure 4.2 we see that our true value is 100 with a filter estimate of 87.0043. This

40

gives a relative error of 0.13. Similarly, for the diffusion coefficient, the filter estimates Dh the

true value of 0.1 to be 0.0768, which yields a relative error of 0.232. The estimated parameters for

carrying capacity and the diffusion coefficient are an underestimate of the true parameters.

Figure 4.2: The true solution and the estimated mean of the filter ensembles of the single-species model using (2.31) and the initial conditions (2.33) for Atlantic herring. This figure also shows the ensemble Kalman filter’s estimate for Kc and Dc. The black line represents the true solution of the parameter. The solid red line represents the estimated value of the parameter over time. The dotted red lines are two standard deviations of error about the estimated parameter. The true and estimated parameter values are shown in Table 4.3.

Parameter True Value Estimated Value Relative Error

Kh 100 87.0043 0.13 Dh 0.1 0.0768 0.232

Table 4.3: Relative error for Atlantic herring single-species PDE estimated parameters.

41

4.4.2 PDE: Multi-species

For the multi-species PDE model, we estimate carrying capacity and the diffusion coefficient for

each species, as well as β. We also attempt to estimate ε.

Meaning Parameter Herring Value Cod Value Mortality rate μi 0.5 0.5 Growth rate scale αi 3 1 Velocity magnitude vi 1 2

Carrying capacity Ki 100 20 Diffusion coefficient Di 0.1 0.1

Mortality from cod β 0.1 N/A Conversion efficiency ε N/A 0.1

Table 4.4: Parameter values used in computing multi-species PDE model solutions, where the parameters we estimate are highlighted in red.

Figure 4.3: The true solution and the estimated mean of the filter ensembles of the single-species model use (2.35) and (2.36) using the initial conditions (2.34) and (2.33) for Atlantic herring and Atlantic cod.

In Figures 4.3 and 4.4, we can see that the Atlantic herring and Atlantic cod ensemble means

follow the same patterns as the true solution to both of these. This verifies that our filter is working

correctly. Moving on to the parameters in 4.5, we can observe what the ensemble Kalman filter

estimates for the parameters. Starting at the carrying capacity for Atlantic herring, Kh, we can see,

by the black line, that the true value of Kh is 100. The filter was able to estimate Kh as 57.4966.

42

Figure 4.4: The true solution and the estimated mean of the filter ensembles use the (2.35) and (2.36) using the initial conditions (2.34) and (2.33) for Atlantic herring and Atlantic cod.

Parameter True Value Estimated Value Relative Error Kh 100 57.4966 0.425 Dh 0.1 0.0437 0.563 Kc 20 20.1249 0.0062 Dc 0.1 0.074 0.26 β 0.1 0.0901 0.099

Table 4.5: Relative error for Atlantic herring and Atlantic cod PDE multi-species model.

This gives us a relative error of 0.425, which is seen in 4.5. For the diffusion coefficient for Atlantic

herring, we can see in 4.5 that the true value is 0.1 and that our filter estimates it to be 0.0437. This

yields a relative error of 0.563, which is seen in 4.5. For the carrying capacity of Atlantic cod,

Kc, we can see that the true value of Kc is represented by the black line in 4.5 and is 20. Our

filter estimates Kc to be 20.1249, which gives a relative error of 0.0062. The diffusion coefficient

for Atlantic cod, Dc, has a true value of 0.1 and the filter estimates it to be 0.074, which gives a

relative error of 0.26. Next, we measure β, which has a true value of 0.1. The filter estimates it to

be 0.0901, which gives a relative error of 0.099. The filter was unable to obtain a useful estimate

of the parameter ε.

43

Figure 4.5: This figure shows the estimated parameters for Kh, Dh, Kc, Dc, and β. The black line represents the true solution of the parameter. The solid red line represents the estimated value of the parameter over time. The dotted red lines are two standard deviations of error about the estimated parameter. The true and estimated parameter values are shown in Table 4.5.

4.4.3 Integrodifference: Single-species

Now, we will observe the integrodifference single-species ensemble Kalman filter results. We will

be estimating carrying capacity and mortality fro each species. First, we will look at the single-

44

species Atlantic cod. In Figure 4.6, the Atlantic cod ensemble mean follows the same pattern as

the true solution, which confirms that our filter is doing what it is supposed to. The graphs for

the estimated parameters Kc and μc in Figure 4.6 are as follows. The true parameters are 50 for

the carrying capacity and 0.2 for the mortality rate. In Figure 4.6, we can see that the filter finds

the parameters Kc and μc to be 41.0108 and 0.1758 respectively. In Table 4.7, the relative error of

the estimated parameters are given. The relative error for Kc = 0.1798 and the relative error for

μc = 0.121. The estimated parameters Kc and μc are an underestimate of the true parameters.

Now, we will look at the Kalman filter results for the Atlantic herring integrodifference model.

In Figure 4.7, the Atlantic herring ensemble mean follows the same pattern as the true solution,

which confirms that our filter is doing what it is supposed to. The graphs for the estimated param-

eters Kh and μh in Figure 4.7 are as follows. The true parameters are 150 for the carrying capacity

and 1.5 for the mortality rate. The true estimates are modeled by the black line in Figure 4.7. In

Figure 4.7, we can see that the filter finds the parameters Kh and μh to be 94.141 and 0.3724 re-

spectively. In Table 4.8, the relative error of the estimated parameters are given. The relative error

for Kh =0.3724 and the relative error for μh = 0.6879. The estimated parameters Kh and μh are an

underestimate of the true parameters.

Meaning Parameter Herring Value Cod Value Mortality rate μi 1.5 0.2 Growth rate scale αi 0.5 10 Velocity magnitude vi 1 1

Carrying capacity Ki 150 20

Table 4.6: Parameter values used in computing single-species integrodifference model solutions, where parameters we estimate are highlighted in red.

45

Figure 4.6: The true solution and the estimated mean of the filter ensembles of the single-species model use (3.1) and the initial conditions (3.6) for Atlantic cod. The black line represents the true solution of the parameter. The solid red line represents the estimated value of the parameter over time. The dotted red lines are two standard deviations of error about the estimated parameter. The true and estimated parameter values are shown in Table 4.7.

46

Parameter True Value Estimated Value Relative Error Kc 50 41.0108 0.1798 μc 0.2 0.1758 0.121

Table 4.7: Relative error for single-species integrodifference Atlantic cod.

Parameter True Value Estimated Value Relative Error Kh 150 94.141 0.3724 μh 1.5 0.4681 0.6879

Table 4.8: Relative error for single-species integrodifference Atlantic herring.

Figure 4.7: The true solution and the estimated mean of the filter ensembles of the single-species model use (3.1) using the initial conditions (3.5) and (3.6) for Atlantic herring and Atlantic cod. The black line represents the true solution of the parameter. The solid red line represents the estimated value of the parameter over time. The dotted red lines are two standard deviations of error about the estimated parameter. The true and estimated parameter values are shown in Table 4.8.

4.4.4 Integrodifference: Multi-species

Now, that we have seen the ensemble Kalman filter estimates for the single-species integrodif-

ference models, we can look at the multi-species parameter estimations. We will be estimating

carrying capacity and mortality rate for each species, as well as β and ε. In Figures 4.8 and 4.9,

the Atlantic herring and Atlantic cod ensemble means follow the same patterns as the true solu-

tions, which confirms that our filter is doing what it is supposed to. The graphs for the estimated

parameters Kh, Kc, μh, μc, β, and ε in Figure 4.10 are as follows. The true parameters are 150 for

Kh, 1.5 for μh, 25 for Kc, 0.5 for μc, and 0.2 for β. The true estimates are modeled by the black

47

line in Figure 4.7.The ensemble Kalman filter estimated the parameters Kh, μh, Kc, μc, and β to

be 124.9427, 1.3687, 16.1985, 0.9395, and 0.0229 respectively. In Table 4.10, the relative error of

the estimated parameters are given. The relative error for Kh = 0.167, Kc = 0.352, μh = 0.0875,

μc = 0.879, and β = 0.145. Unfortunately, our ensemble Kalman was unable to estimate the pa-

rameter ε. The estimated parameters Kh, Kc and μh are an underestimate of the true parameters.

The estimated parameters μc and β is an overestimate of the true parameter.

Meaning Parameter Herring Value Cod Value Mortality rate μi 1.5 0.5 Growth rate scale αi 0.5 0.5 Velocity magnitude vi 1 1

Carrying capacity Ki 150 25 Mortality from cod β 0.02 N/A Conversion efficiency ε N/A 0.01

Table 4.9: Parameter values used in computing multi-species integrodifference model solutions, where parameters we estimate are highlighted in red.

Figure 4.8: The true solution and the estimated mean of the filter ensembles of the multi-species model use (3.7) and (3.8) with the initial conditions (3.11) and (3.12) for Atlantic herring and Atlantic cod. Parameter values are shown in Table 4.9.

48

Figure 4.9: The true solution and the estimated mean of the filter ensembles of the multi-species model use (3.7) and (3.8) with the initial conditions (3.11) and (3.12) for Atlantic herring and Atlantic cod. Parameter values are shown in Table 4.9.

Parameter True Value Estimated Value Relative Error Kh 150 124.9427 0.167 μh 1.5 1.3687 0.0875 Kc 25 16.1985 0.352 μc 0.5 0.9395 0.879 β 0.02 0.0229 0.145

Table 4.10: Relative error for Atlantic herring and Atlantic cod ID multi-species model.

49

Figure 4.10: This figure shows the estimated parameters for Kh, μh, Kc, μc, and β. The black line represents the true solution of the parameter. The solid red line represents the estimated value of the parameter over time. The dotted red lines are two standard deviations of error about the estimated parameter. As time progresses, the standard deviations become smaller because our filter is more confident in finding the best estimated value for the provided data. The true and estimated parameter values are shown in Table 4.10.

50

Chapter 5

Model Comparison

5.1 Comparison Method

After both the single-species and multi-species forms of the integrodifference models and the PDE

were all set, we determined a comparison technique. Our comparison technique utilizes synthetic

data, as well as single-species and multi-species models. To compare the single-species models

with the multi-species models, we first gather the synthetic data that was created and used in the

PDE or integrodifference multi-species model. Then, we insert this data into appropriate single-

species for either Atlantic herring or Atlantic cod, depending on which one is being compared.

Then the single-species Kalman filter is run with the multi-species data. The posterior is taken,

which is the last mean of the parameter estimates for the parameters that are being estimated (car-

rying capacity, K, and the diffusion coefficient, D for PDE and carrying capacity, K, and mortality,

μ for integrodifference).

Now, we run the appropriate single-species model, either Atlantic herring or Atlantic cod and

compare the output of this model to the true solution of the multi-species model. To compare

we take the output of the regular single-species model and subtract the multi-species true solution

and take the absolute value of them. This will give the absolute error. The true solution of the

51

multi-species model is generated from plugging in all of the true parameters into the multi-species.

5.2 PDE Comparison

In Figure 5.1, the PDE model comparison for Atlantic herring, it is evident that the population

of Atlantic herring in the single-species model is greater than in the multi-species model. In the

single-species model, the Atlantic herring grow during their spawning season, which is seen in

the sharp increases and decreases of the graph. The multi-species true solution has less Atlantic

herring, presumably because of the Atlantic cod eating them. Therefore, the population of Atlantic

herring does not grow as much in the multi-species true solution. The absolute error shows this

discrepancy.

Figure 5.1: This is the comparison for the single-species and multi-species Atlantic herring PDE model using the equation (2.31) and initial condition (2.33).

52

In Figure 5.2, the PDE model comparison for Atlantic cod, the single-species model seems

to grow less than the multi-species true solution does. In the single-species solution, it is evident

through the sharp increase and decreases that the Atlantic cod population is growing during the

spawning seasons. However, in the multi-species true solution, it appears that the population is

growing more, presumably due to consumption of the Atlantic herring. In the absolute error, we

see the discrepancy in the population growth.

5.3 Integrodifference Comparison

In Figure 5.3, the integrodifference Atlantic herring comparison, the single-species model allows

for the population of herring to grow and recover, whereas the multi-species does not. In the

Figure 5.2: This is the comparison for the single-species and multi-species Atlantic cod PDE model using the equation (2.31) and initial condition (2.34).

53

Figure 5.3: This is the comparison for the single-species and multi-species Atlantic herring inte- grodifference model using the equation (3.1) and initial condition (3.5).

single-species prediction, the sharp increases and decreases represent the population growth during

spawning seasons. The population decreases when the fish are not spawning, but it can recover

when they start to spawn again. This is not seen in the multi-species true solution. When there

is the interaction between the Atlantic cod and the Atlantic herring, the Atlantic herring are being

eaten by the Atlantic cod and dying out. The population is not able to recover because they are

being continuously eaten. In the absolute error, there is less error initially because the initial

conditions are the same. The first couple years also have less error because the population of cod

in the multi-species model is able to recover up until around year 3. Then the herring die out. The

single-species model seems to be overestimating the population of Atlantic herring.

In Figure 5.4, the integrodifference Atlantic cod comparison, observe that in the single-species

prediction the Atlantic cod stay more between the first and second spaces. In the multi-species

54

Figure 5.4: This is the comparison for the single-species and multi-species Atlantic cod integrod- ifference model using the equation (3.1) and initial condition (3.6).

true solution, the Atlantic cod are spreading to the third and fourth spaces, as well as the spaces

between zero and one as eat the Atlantic herring. This is easily seen in the absolute error. The

most discrepancy between the single-species prediction and the multi-species true solution occurs

along the spaces three and four. In spaces between one and two, the single-species model esti-

mates the population with less discrepancy with the multi-species true solution. However, in those

outer spaces, the single-species model does not account for the Atlantic cod following the Atlantic

herring.

55

Chapter 6

Discussion

6.1 Summary

The goal of this paper is to compare single-species and multi-species models in the context of

NOAA Fisheries stock assessments. We create single and multi-species PDE and integrodifference

models for the Atlantic cod and Atlantic herring populations in the Georges Bank region. Many

of the parameters used in population modeling are poorly known for the Atlantic cod and Atlantic

herring due to difficulty of measurement. To account for this, we use an ensemble Kalman filter to

estimate carrying capacity, predation rate, and conversion efficiency for both model types as well

as the diffusion coefficients in the PDE models and mortality rates in the integrodifference models.

To compare the single-species and multi-species models, we generate synthetic data by adding

noise to the output of each type of multi-species model and use this as our observation data in the

ensemble Kalman filter for the single-species models of the same type. We then run the single-

species model with the parameters estimated in the filter and take the absolute error of the single-

species model prediction and the true solution used to generate the synthetic data.

56

6.2 Interpretation of Results

Between the two types of models, the PDE estimates true parameter values for carrying capacity

and predation rate better than the integrodifference, though both types of model estimate the pre-

dation rate with a relative error of less than 0.2. For the Atlantic cod, error in carrying capacity is

almost entirely from underestimation rather than overestimation. This pattern is less clear for the

Atlantic herring.

For the Atlantic cod, the multi-species PDE model estimates all shared parameters more closely

than the single-species. For the integrodifference, the single-species estimates all shared param-

eters better than the multi-species. For the herring, the opposite is true. The single-species PDE

model estimates parameters more closely than the multi-species for the Atlantic herring, but the

multi-species integrodifference estimates more closely than the single-species.

We use a variety of ranges for the prior distributions of the parameters in the ensemble Kalman

filters, and the estimated parameters result in very similar model predictions for all of the models.

In the comparisons, single-species models overestimated the Atlantic herring and underestimated

the Atlantic cod for both the PDE and the integrodifference models.

6.3 Future Work

There are still many interesting questions relating to this project that can be addressed in future

studies. Here we discuss these questions as well as suggested directions for further exploration.

We were provided with almost 50 years of survey data by the NEFSC including measurements

such as fish abundance, water temperature, season, and year. We initially planned to use this data

in our ensemble Kalman filter after analyzing the synthetic data, but we found that the data was

too jagged and our filter did not respond well. In order to utilize the data, we would need to

find some way to make it smoother. One option suggested by a NEFSC employee would be to

analyze the data on a log scale. Additionally, the NEFSC collects data twice per year, and we

57

mimicked this in our synthetic data. It is possible that more frequent observations could improve

our filter estimates for some parameters. This could be tested by generating synthetic data more

frequently than twice per year, running the ensemble Kalman filter, and comparing the relative

errors of parameter estimates using both more frequent and less frequent data.

There are a variety of parameters in the models we developed, and not all of them may be able

to be well-estimated using the filter given the sparsity of the data. We could perform sensitivity

analysis [20] to see which subset of parameter values in each model type most affects the model

output and focus on estimating those, and we could set the least sensitive parameters to constant

values.

There are many options for modeling population dynamics such as growth and predation in

both the PDE and integrodifference as well as many options for kernels in the integrodifference

models. One option we considered but did not attempt was using a Ricker [17] or Beverton-

Holt [13] growth function instead of the logistic. A Laplace kernel could also be used instead of a

Gaussian kernel in the integrodifference model [21]. A variety of functions could be used instead

of the versions used in this paper to represent velocity and birth rate. In the integrodifference

model, some of the dynamics we placed outside the integral could be edited and included in the

integrand.

Additionally, the PDE model does not account well for schooling, which is exhibited strongly

by the Atlantic herring. Incorporating a feature to model this behavior could be significant to

predicting the Atlantic herring’s population, and it could counter the tendency of the PDE model to

predict quick decreases in population due to diffusion which may not be prevalent in the ecosystem.

All of the models in this paper examine either one or two species of fish. There are, of course,

many more species of fish in Georges Bank whose behavior may be relevant to Atlantic cod and

Atlantic herring populations. For example, the spiny dogfish and silver hake compete with the

Atlantic cod to eat the Atlantic herring, but they are also eaten by the Atlantic cod.

One could expand on this project by developing a model for three or more of these species,

58

generating data with the model including the most species, and repeating the comparison in this

paper for each model using fewer species. For example, a three-species model could be used to

generate data which could be compared against the species-pair model and single-species models

developed in this paper.

Atlantic herring and Atlantic cod both have spawning ranges. While the models in this paper

account for a spawning season with migration before and after, they all assume that spawning

occurs at the same rate at every location. This may not be an accurate representation of fish

spawning. One could easily add a specification that spawning occur only within a certain spatial

range.Additionally, the models in this paper examine only one dimension. Georges Bank is a three-

dimensional region, and fish will at times move towards or away from the shore or to deeper or

shallower water to find a more desirable temperature instead of moving directly along the coast.

The models could be expanded to account for three dimensions, but the process may be very

complex.

The model comparisons used give an absolute error, but this paper does not include a maximum

allowable error. If a maximum error were chosen, they could be used to provide a definitive

assessment of whether the models developed here show a significant improvement from single-

species to multi-species or whether single-species are sufficient.

59

References

[1] J. Beddington, D. Agnew, and C. Clark, “Current Problems in the Management of Marine

Fisheries,” Science, vol. 316, no. 5832, pp. 1713 – 1716, 2007.

[2] “Atlantic Cod,” https://www.fisheries.noaa.gov/species/atlantic-cod, 2018.

[3] A. Myers, N. Hutchings, and N. Barrowman, “Hypotheses for the decline of cod in the North

Atlantic,” Marine Ecology Progress Series, vol. 138, no. 293-308, 1996.

[4] R. O’Boyle, C. Francis, N. Hall, and N. Klaer, “SARC 54 PANEL SUMMARY REPORT,”

June 2012.

[5] J. Link, R. Gamble, and M. Fogarty, “An Overview of the NEFSC’s Ecosystem Modeling

Enterprise for the Northeast US Shelf Large Marine Ecosystem: Towards Ecosystem-based

Fisheries Management,” October 2011.

[6] “NEFSC Toolbox,” http://nft.nefsc.noaa.gov/Comparing.html, May 2016.

[7] E. Olsen, G. Fay, S. Gaichas, R. Gamble, S. Lucey, and J. Line, “Ecosystem Model Skill

Assessment. Yes We Can!” Plos One, vol. 11, no. 1, 2016.

[8] P. Politics, J. Galbraith, P. Kostovick, and R. Brown, “Northeast Fisheries Science Center

Bottom Trawl Survey Protocols for the NOAA Ship Henry B. Bigelow,” 2014, Northeast

Fisheries Science Center Reference Document.

60

[9] H. Bigelow and W. Schroeder, Fishes of the Gulf of Maine. US Government Printing Office,

1953, vol. 53.

[10] “Atlantic Herring,” https://www.fisheries.noaa.gov/species/atlantic-herring, 2018.

[11] K. Kanwit, “Atlantic Herring Tagging: Insights into Migration and Movement,” 2006, North-

east Fisheries Science Center Reference Document.

[12] M. Morin, “Movement of Atlantic Cod in And Among the Western Gulf of Maine Rolling

Closures as Determined Through Mark and Recapture,” Master’s thesis, University of New

Hampshire, 2000.

[13] L. Edelstein-Keshet, Mathematical Models in Biology, 1st ed. SIAM: Society for Industrial

and Applied Mathematics, 2005.

[14] R. Haberman, Elementary Applied Partial Differential Equations, 2nd ed. Pentice-Hall,

INC, 1987.

[15] R. Leveque, Finite difference methods for ordinary and partial differential equations: steady-

state and time-dependent problems. Society for Industrial and Applied Mathematics, 2007,

vol. 98.

[16] N. Marculis and R. Lui, “Modeling the Biological Invasion of Carcinus maenas,” Journal of

Biological Dynamics, vol. 10, no. 1, pp. 140–163, 2015.

[17] M. Kot and W. Schaffer, “Discrete-Time Growth-Dispersal Models,” Mathematical Bio-

sciences, vol. 80, no. 109-136, 1986.

[18] A. Arnold and A. Lloyd, “An approach to periodic, time-varying parameter estimation using

nonlinear filtering,” To appear in Inverse Problems, 2018.

61

[19] A. Arnold, D. Calvetti, and E. Somersalo, “Parameter estimation for stiff deterministic dy-

namical systems via ensemble Kalman filter,” Inverse Problems, vol. 30, no. 10, 2014.

[20] D. M. Hamby, “A review of techniques for parameter sensitivity analysis of environmental

models,” Environmental Monitoring and Assessment, vol. 32, no. 2, pp. 135–154, 1994.

[21] M. Neubert and M. Lewis, “Dispersal and Pattern Formation in a Discrete-Time Predator-

Prey Model,” Theoretical Population Biology, vol. 48, pp. 7–43, 1995.

62

Appendix A

Matlab Code

A.1 Partial Differential Equation Model Codes

1 %Single species PDE model main file for Atlantic Cod

23 clear;clc;close all;

4 %% Define parameters

5 cod parameters=load('Cod parameters.txt'); % load in .txt file

6 K c = cod parameters(1); %Carrying capacity

7 mu c = cod parameters(2); %Fishing mortality

8 D c = cod parameters(3); %Diffusion constant

9 a c = cod parameters(4); %Advection constant

10 mag c = cod parameters(5); % scaling factor for velocity

1112 %% Time discretization

13 time space = load('time space parameters.txt'); % load .txt file

14 k = time space(1); % time step

15 t end = 3; % end time

63

16 time = 0:k:t end; % time vector

17 ntime = length(time); % length of time vector

1819 k2 = .5\*kˆ2; % bootstrapping time step

20 t bar = 0:k2:k; % bootstapping time vector

21 nt bar = length(t bar); % length of bootstapping time vector

2223 %% Spatial discretization

24 h = time space(3); % space step

25 x end = time space(4); % end space

26 space = 0:h:x end; % space vector

27 nspace = length(space); % length of space vector

28 M = nspace;

2930 %% Define common constants

31 r = k/(2\*h\*h);

32 d con = D c\*r; %Constant arising from the Crank-Nicolson

3334 %% Call the birth rate function alpha

35 [alpha c,t period] = AlphaC SS(k,t end,a c); %Returns a vector alpha c containing

36 %the value of the growth rate at each time

3738 %% Define relevant matrices

3940 %Coefficient matrix due to Crank-Nicolson for Vˆn+1

41 CN left = -d con\*diag(ones(M-1, 1), 1) + 2\*d con\*diag(ones(M,1)) ...

42 - d con\*diag(ones(M-1, 1), -1);

43 CN left(1,2) = 2\*CN left(1,2); %Impose zero-slope boundary condition

44 CN left(end,end-1) = 2\*CN left(end,end-1);

45 %Identity matrix to represent the time approx for Vˆn+1

46 Forward time left = diag(ones(M,1));

64

4748 %Total matrix with the coefficients of the solution at time n+1

49 M lhs = Forward time left + CN left;

5051 %Coefficient matrix due to CN for Vˆn

52 CN right = d con\*diag(ones(M-1, 1), 1) - 2\*d con\*diag(ones(M,1)) ...

53 + d con\*diag(ones(M-1, 1), -1);

54 %Impose zero-slope boundary condition

55 CN right(1,2) = 2\*CN right(1,2);

56 CN right(end,end-1) = 2\*CN right(end,end-1);

5758 %Identity matrix representing the Vˆn term due to the time approx

5960 Forward time right = diag(ones(M,1));

6162 M rhs base = Forward time right + CN right;

636465 %% Bootstrapping matrices

66 r2 = k2/(2\*h\*h);

67 d con2 = D c\*r2; %Constant arising from the Crank-Nicolson

6869 %Coefficient matrix due to Crank-Nicolson for Vˆn+1

7071 CN left2 = d con2\*CN left/d con;

72 %Identity matrix to represent the time approx for Vˆn+1

73 Forward time left2 = diag(ones(M,1));

7475 %Total matrix with the coefficients of the solution at time n+1

76 M lhs2 = Forward time left2 + CN left2;

77

65

78 %Coefficient matrix due to CN for Vˆn

7980 CN right2 = d con2\*CN right/d con;

8182 %Identity matrix representing the Vˆn term due to the time approx

8384 Forward time right2 = diag(ones(M,1));

8586 M rhs2 base = Forward time right2 + CN right2;

878889 %% Initial and boundary conditions

9091 IC = (space.\*(3-space)).ˆ6.\*normpdf(space,0,1)+10;

92 %g0 row = zeros(1, ntime); %Have not yet found g0 and g1

93 %g1 row = zeros(1, ntime);

9495 %% Define the solution matrix

9697 V save = zeros(M, ntime); %Creates a matrix to store values for V in

98 V save(:,1) = IC'; %Changes the first column to the initial conditions

99

100

101 %% Define the Bootstrapping solution matrix

102

103 V bar = zeros(M,nt bar); %Matrix to store the bootstrapping solutions in

104 V bar(:,1) = IC'; %Sets same initial condition for bootstrapping matrix as

105 %in the other matrix

106

107

108 %% Update by time step

66

109 for n=1:ntime-1

110

111 %run('velocity c.m')

112 v c = velocity c(n,k,t end);

113 a con = v c\*k/h; %Constant arising from upwinding

114 UW right = a con\*diag(ones(M-1, 1), -1) - a con\*diag(ones(M,1));

115

116 %Impose zero-slope boundary conditions

117 UW right(1,:) = 0;

118 UW right(end,:) = 0;

119 %Define the reaction term

120 React right = (k\*alpha c(n) - k\*mu c)\*diag(ones(M,1));

121

122 a con2 = v c\*k2/h; %Constant from upwinding with boostrap matrices

123 UW right2 = a con2\*diag(ones(M-1, 1), -1) - a con2\*diag(ones(M,1));

124

125 %Impose zero-slope boundary conditions

126 UW right2(1,:) = 0;

127 UW right2(end,:) = 0;

128 React right2 = (k2\*alpha c(n) - k2\*mu c)\*diag(ones(M,1));

129

130 %Assemble total matrices

131

132 M rhs = M rhs base + UW right + React right;

133 M rhs2 = M rhs2 base + UW right2 + React right2;

134

135 %Implement bootstrapping when overall time loop is on first iteration

136 if n == 1

137 for m=1:nt bar-1

138

139 V bar(:,m+1) = M rhs2\*V bar(:,m) - ...

67

140 (k2\*alpha c(n)/K c)\*V bar(:,m).\*V bar(:,m);

141

142 V bar(:,m+1) = M lhs2\V bar(:,m+1);

143 end

144

145 V save(:,2) = M rhs\*V bar(:,end) - ...

146 (k\*alpha c(n)/K c)\*V bar(:,end).\*V bar(:,end);

147

148 V save(:,2) = M lhs\V save(:,2);

149

150 else

151 %When you're done with bootstrapping, update normally

152

153 V save(:,n+1) = M rhs\*V save(:,n) - ...

154 (k\*alpha c(n)/K c)\*V save(:,n).\*V save(:,n);

155

156 V save(:,n+1) = M lhs\V save(:,n+1);

157

158 end

159

160 end

161

162

163 %% Plot

164 figure(1);

165 surf(time,space,V save)

166 %view(2);

167 xlabel('time'); ylabel('space'); zlabel('\rho(x,t)');

168 title('Atlantic Cod');

169 set(gca,'FontSize',20);

170 shading interp

68

171 colorbar

1 % Multi-species PDE model for Atlantic cod and Atlantic herring

23 clear;clc;close all;

45 %% Define parameters for cod

6 parameters=load('Multispecies parameters.txt'); % load values from .txt file

7 K c = parameters(1); %Carrying capacity

8 mu c = parameters(2); %Fishing mortality

9 D c = parameters(3); %Diffusion constant

10 a c = parameters(4); %Alpha scaling factor

11 mag c = parameters(5); % Velocity scaling term

1213 %% Define parameters for herring

14 K h = parameters(6); %Carrying capacity

15 mu h = parameters(7); %Fishing mortality

16 D h = parameters(8); %Diffusion constant

17 a h = parameters(9); %Alpha scaling factor

18 mag h = parameters(10); %Velocity magnitude

1920 %% Define predator-prey parameters

21 beta = parameters(11); %Predation rate

22 epsilon = parameters(12); %Conversion efficiency

2324 %% Time discretization

25 time space = load('time space parameters.txt');

26 k = time space(1); % time step

27 t end = time space(2); % end time

28 time = 0:k:t end; % time vector

69

29 ntime = length(time); % length of time vector

3031 k2 = .5\*kˆ2; % bootstrapping time step

32 t bar = 0:k2:k; % bootstrapping time vector

33 nt bar = length(t bar); % length of bootstrapping time vector

3435 %% Spatial discretization

36 h = time space(3); % space step

37 x end = time space(4); % end space

38 space = 0:h:x end; % space vector

39 nspace = length(space); % length of space vector

40 M = nspace;

4142 %% Define common constants

43 r = k/(2\*h\*h);

44 d con c = D c\*r; %Constant arising from the Crank-Nicolson for cod

45 d con h = D h\*r; %Constant arising from the Crank-Nicolson for herring

4647 %% Call birth rate functions

48 [alpha c,¬] = AlphaC SS(k,t end,a c); %Birth rate vector for cod

49 [alpha h,t period] = AlphaH AA(k,t end,a h); %Birth rate vector for herring

5051 %% Define relevant matrices

5253 %Coefficient matrix due to Crank-Nicolson for Vˆn+1

54 CN quadrant = diag(ones(M-1, 1), 1) - 2\*diag(ones(M,1)) + diag(ones(M-1, 1), -1);

5556 %Impose zero-slope boundary conditions

57 CN quadrant(1,2) = 2\*CN quadrant(1,2);

58 CN quadrant(end,end-1) = 2\*CN quadrant(end,end-1);

59

70

60 CN right = [d con h\*CN quadrant,zeros(M);zeros(M),d con c\*CN quadrant];

61 CN left = -1\*CN right;

6263 %Identity matrix to represent the time approx for Vˆn+1

64 Forward time left = diag(ones(2\*M,1));

6566 %Total matrix with the coefficients of the solution at time n+1

67 M lhs = Forward time left + CN left;

6869 %Identity matrix representing the Vˆn term due to the time approx

7071 Forward time right = diag(ones(2\*M,1));

7273 M rhs base = Forward time right + CN right;

7475 %% Bootstrapping matrices

76 r2 = k2/(2\*h\*h); %Redefine constants with the bootstrapping time step

77 d con2 c = D c\*r2;

78 d con2 h = D h\*r2;

7980 %Coefficient matrix due to Crank-Nicolson for Vˆn+1

8182 CN right2 = [d con2 h\*CN quadrant,zeros(M);zeros(M),d con2 c\*CN quadrant];

83 CN left2 = -1\*CN right2;

84 %Identity matrix to represent the time approx for Vˆn+1

85 Forward time left2 = diag(ones(2\*M,1));

8687 %Total atrix with the coefficients of the solution at time n+1

88 M lhs2 = Forward time left2 + CN left2;

8990 %Identity matrix representing the Vˆn term due to the time approx

71

9192 Forward time right2 = diag(ones(2\*M,1));

9394 M rhs2 base = Forward time right2 + CN right2;

9596 %% Alpha/carrying capcity and beta/epsilon matrices

9798 %Matrices to represent interspecies term coefficients

99

100 BetaEpsilon = k\*[-1\*beta\*eye(M),zeros(M);zeros(M),epsilon\*eye(M)];

101 BetaEpsilon2 = k2\*[-1\*beta\*eye(M),zeros(M);zeros(M),epsilon\*eye(M)];

102

103 %% Initial and boundary conditions

104

105 IC1 = 5\*(space.\*(3-space)).ˆ6.\*normpdf(space,0,1)+10;

106 IC2 = (space.\*(3-space)).ˆ6.\*normpdf(space,0,1)+10;

107

108 %% Define the solution matrix

109

110 V save = zeros(2\*M, ntime); %Creates a matrix to store values for V in

111 V save(1:M,1) = IC1'; %Changes the first column to the initial conditions

112 V save(M+1:end,1) = IC2';

113

114 %% Define the Bootstrapping solution matrix

115

116 V bar = zeros(2\*M,nt bar); %Creates a matrix to store bootstrapping values

117 V bar(1:M,1) = IC1'; %Changes the first column to initial conditions

118 V bar(M+1:end,1) = IC2';

119

120 %% Update by time step

121 for n=1:ntime-1

72

122

123 v c = velocity c(n,k,t end);

124 v h = velocity h(n,k,t end);

125

126 a con c = v c\*k/h; %Constant arising from upwinding

127 a con h = v h\*k/h;

128

129 %Define the matrix representing upwinding for a single species

130 UW quadrant = diag(ones(M-1, 1), -1) - diag(ones(M,1));

131 %Impose zero-slope boundary conditions

132 UW quadrant(1,:) = 0;

133 UW quadrant(end,:) = 0;

134

135 %Combine the UW quadrant matrices for each species into one matrix

136 UW right = [a con h\*UW quadrant,zeros(M);zeros(M),a con c\*UW quadrant];

137

138 React right = [(k\*alpha h(n) - k\*mu h)\*diag(ones(M,1)),...

139 zeros(M);zeros(M),(k\*alpha c(n) - k\*mu c)\*diag(ones(M,1))];

140

141 %Repeat the setup with the bootstrapping time step

142 a con2 c = v c\*k2/h;

143 a con2 h = v h\*k2/h;

144 UW right2 = [a con2 h\*UW quadrant,zeros(M);...

145 zeros(M),a con2 c\*UW quadrant];

146

147 React right2 = [(k2\*alpha h(n) - k2\*mu h)\*diag(ones(M,1)),zeros(M);...

148 zeros(M),(k2\*alpha c(n) - k2\*mu c)\*diag(ones(M,1))];

149

150 M rhs = M rhs base + UW right + React right;

151 M rhs2 = M rhs2 base + UW right2 + React right2;

152

73

153 V save flip = [V save(M+1:end,n);V save(1:M,n)];

154 AlphaK = k\*[(alpha h(n)/K h)\*eye(M),zeros(M);zeros(M),...

155 (alpha c(n)/K c)\*eye(M)];

156 AlphaK2 = k2\*[(alpha h(n)/K h)\*eye(M),zeros(M);zeros(M),...

157 (alpha c(n)/K c)\*eye(M)];

158

159 %Implement bootstrapping when time loop is on first iteration

160 if n == 1

161 for m=1:nt bar-1

162 V bar flip = [V bar(M+1:end,m);V bar(1:M,m)];

163 V bar(:,m+1) = M rhs2\*V bar(:,m) - AlphaK2\*V bar(:,m).\*V bar(:,m)...

164 + BetaEpsilon2\*V bar(:,m).\*V bar flip;

165

166 V bar(:,m+1) = M lhs2\V bar(:,m+1);

167 end

168

169 V save(:,2) = M rhs\*V bar(:,end) - AlphaK\*V bar(:,end).\*V bar(:,end)...

170 + BetaEpsilon\*V bar(:,end).\*V bar flip;

171

172 V save(:,2) = M lhs\V save(:,2);

173

174 else

175

176 %Continue using regular time step after bootstrapping

177

178 V save(:,n+1) = M rhs\*V save(:,n) - AlphaK\*V save(:,n).\*V save(:,n)...

179 + BetaEpsilon\*V save(:,n).\*V save flip;

180

181 V save(:,n+1) = M lhs\V save(:,n+1);

182

183 end

74