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# Understanding Changes in Marine Communities Through a Discretized, Size-Structured Matrix Model

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## Abstract

We study a discretized, size-structured matrix model which calculates population in a marine community over time. A portion of this model is a discretized version of the McKendrick-von Foerster equation, so we spend some time studying the process of discretizing that equation. We implement a mini model containing 10 size categories instead of the original 50, and we looked at how the marine community behaves over 40 years. We discuss some of the challenges when implementing this model.

## 1 Introduction

The science community is interested in predicting what could happen to a marine community over time using data on what is currently happening to that community. A good model can help us investigate and predict how a general marine community interacts with both environmental change and humans [1, 4]. We can do this by including factors which account for these interactions. Therefore, populations can be predicted and explained by several variables, depending on what is being studied. Humans harvest marine communities by collecting marine life for commercial use such as fishing and ingredients for products. Models can thus be used to aid in the protection of marine communities while allowing people to continue to harvest from them.

In this paper, we will examine a marine population model that encompasses an entire ocean ecosystem, breaking down the ecosystem by mass of individuals. Xia and Yamakawa [10] developed this detailed discrete model based off of the McKendrick-von Foerster equation. They ran simulations of a population over 40 years, varying certain parameters. To better understand the full model, we developed a simplified mini model.

The McKendrick-von Foerster equation is a partial differential equation which determines population based on age and time. If we take  $n(t, a)$  as the population in terms of age  $a$  and time  $t$  we get the following relationship:

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -m(a)n, \tag{1}$$

where  $m(a)$  represents the percentage of individuals in the population at age  $a$  who die. This equation was discovered separately by Anderson Grey McKendrick in 1926 when studying applications of epidemiology and again by Heinz von Foerster in 1959 while studying cell cycles [9]. This equation is also easily amended to fit different populations [2]. Though relatively new, the equation has been since used for many research applications relating to populations as we will see in the Applications section.

The paper is laid out as follows. In Section 2, we will introduce the discretization of ordinary differential equations. We will go through the process of discretizing time  $t$  and a variable  $x$  which serves as a measurement of growth. We will also discuss the importance and usefulness of discretizing. Section 3 contains information about the McKendrick-von Foerster equation, including an interpretation of its parts and its application in the model we are studying [10]. We will include discretizing the von Foerster equation and understanding how Xia and Yamakawa discretized their version of the von Foerster equation [10]. In Section 4, we introduce the marine population model which we are studying. This section contains information about the structure and purpose of the model. Section 5 focuses on introducing the mini model we made based off of the model in section 4. This section includes information about the issues we came across while implementing the model. It also includes the results we found once we corrected those issue. Finally, Section 6 contains conclusions we drew from our results and touches on what could be done if we had more time or were to continue this project.

## 1.1 Applications

The McKendrick-von Foerster equation is applied in many different types of papers and experiments. Some of these experiments include studying life cycles, populations, growth tracking, and death populations. As done by Xia and Yamakawa in their 2018 paper [10], one way we can model a population is by using the McKendrick-von Foerster equation, which includes independent variables age and time. This partial differential equation made up of the independent variables age and time can also be easily altered to account for variables that may affect a population.

A paper written by Luca Rossini *et al.* [6] focused on the complete life cycle of an insect. The paper aims to compare a Distributed Delay Model and the McKendrick-von Foerster equation based on their interpretations of an age-based population. In this model, the researchers separated the insects' growth into  $h$  distinct stages. These  $h$  stages are specific times in the insect's life cycle, represented in days. This is a discretization of the age variable. In this case,  $\partial n / \partial a$  becomes a difference quotient measuring the change in population at given stage, including those who are moving into this stage and those who are growing out of this stage. A model like this is a distributed delay model: it tracks discrete ages over time. Rossini *et al.* use these comparisons to better understand the ability of insects to survive. They also use the comparisons to better understand the model's ability to track the subject's survival [6].

The equation can also be applied to cells. For example, Minkevich and Abramychev [3] used a model like the McKendrick-von Foerster equation to track the division of cells and assigned them specific ages over time. They wanted to study how many cells divide and at what age they divide. Cell division is referring to the splitting of cells to make more copies of itself. In this model, both age and time are continuous. They also look into the substrate concentration. The substrate concentration is essentially how much energy is able to be created for the cells use. The substrate concentration correlated heavily with the cells' time and rate of division. In their version of the McKendrick-von Foerster equation, the term  $m(a)$  is in terms of the substrate concentration  $S$  as well as age  $\tau$ . Also, they factor in a dilution rate  $D$ , and instead of looking at the death function  $m(a)$  as percent deaths, they are looking at a specific rate of cell division  $W$ . Because of these modifications to  $m(a)$ , the model is slightly more complicated compared to the McKendrick-von Foerster equation. They did find a positive relationship between cell division and the substrate concentration [3]. As the concentration increases, cell division can occur more often and more quickly.

Another interesting case is a study done on beetles by Rojano *et al.* [5]. Their variation of the McKendrick-von Foerster was

$$\frac{\partial n}{\partial t} + r(T) \cdot \frac{\partial n}{\partial a} = v(T) \cdot \frac{\partial^2 n}{\partial a^2},$$

where  $r(T)$  is the rate of development as a function of temperature. Notice that the right-hand side is the death function, depending on temperature  $T$ , and the second order partial (how quickly the beetle's age development is changing). In this case, temperature was key because they found that eggs, larva, and pupa survived better at different temperatures [5].

Each of these papers show that there are many applications using models based off of the McKendrick-von Foerster equation with different discrete and continuous variable combinations. Xia and Yamakawa compare the characteristics of the McKendrick-von Foerster equation to their own, and they express that their model makes non-observable sub-stages for age [10]. The von-Foerster equation's stages are observable, but their time intervals are not constant. These as well as the Xia and Yamakawa paper show that models based of the McKendrick-von Foerster equation can be molded to fit different studies and they can become very complex quickly.

## 1.2 Importance of Discretizing

Xia and Yamakawa used a discrete model based off of the McKendrick-von Foerster equation. However, the McKendrick-von Foerster equation contains variables which are not discrete. Therefore, sometimes we choose to discretize variables in an equation. We discretize differential equations for several reasons. Discretizing differential equations can better our understanding of the variables within the equation and the relationship between those variables.

Firstly, from a mathematical perspective, we cannot explicitly solve all ordinary differential equations or partial differential equations. Since we can't explicitly solve certain differential equations, we cannot get exact solutions for the differential equations. In these cases, we must discretize the differential equation so we can use methods such as Euler's method to numerically estimate solutions to differential equations.

From a researcher's perspective, when we collect data, we can only realistically measure time in discrete time units. Taking continuous measurements is extremely time consuming, money consuming, unnecessary for understanding the changes within say an animals life span, and sometimes impossible. To understand what happens in an animal's life span does not normally depend on every little nuance that a continuous model would provide. Therefore, most data collected is discrete. Also, if we were tracking age, we are usually not interested in a person when they are exactly  $\pi$  years old. Instead, we could break age into categories of discrete time; this would mean we have a category for people ages 0-1, 1-2, 2-3, 3-4, and so on. Plus, more involved models might have features which depend on age. An example would be that female humans can only reproduce from about the age 13 to age 55, and in this span, females will more likely reproduce in a smaller subset of age, say 25 to 35.

Another reason to discretize is the fact that we cannot realistically have half a person. A person is either counted or not. Because of this, the population is not continuous because we would need integer values. Also, the continuous version is an approximation, not exact. Therefore, we are at an advantage using the discretized version because the data counts in integers, and the data we receive is exact.

## 2 Discretization of Differential Equations

Differential equations are equations with one or more continuous variables. However, continuous variables might not be ideal because we want to look at specific intervals of a variable, or we the results we receive are not realistic. Discretizing a differential equation transforms continuous variables into discrete variables. Sometimes, we can better understand variables in a model when they are discrete variables. Other times we want to use a differential equation that is not explicitly solvable, so we must be discretize the equation in order to numerically approximate solutions. We must note that models can be continuous or discrete. Both continuous and discrete models can be useful depending on how we want to model data. For example, later in the paper we will discuss size categories. This is an example of where a discrete model would be more beneficial to use. Another example would be when we are collecting data on a population over time. We do not need the second-by-second detail of a population as it can distract from what is going on in the population overall. Instead, we would represent time discretely. We will discuss more on a discrete model in Section 4.

We will start by discretizing this ordinary differential equation:

$$\frac{dx}{dt} = f(t, x). \quad (2)$$

We will interpret  $t$  as time and  $x = x(t)$  as a function dependent on time, say a population size at time  $t$ . We first discretize the variable  $t$ . We take  $\Delta t$  to be a time increment, for example one month. Let's call our starting time  $t_0$ . We can define times  $t_1, t_2, \dots$  recursively as follows:

$$t_{n+1} = t_n + \Delta t. \quad (3)$$

We can think of each time  $t_n$  being the first day of a month. Then the change in time from two months to three months is  $\Delta t = t_3 - t_2$ .

The population  $x_n = x(t_n)$  would be the population at the start of the  $n$ th month. The corresponding population change to our previous time change example is  $\Delta x = x_3 - x_2$ . Note that  $\Delta x$  is not constant in the same way  $\Delta t$  is because in general a population does not change each month by the same amount. We can think of  $\Delta x$  as the change in  $x$  over some change in time  $\Delta t$ . We can use this to compute the average rate of change of  $x$ , given by  $\Delta x / \Delta t$ . If  $\Delta t$  is small enough, the average rate of change of  $x$  is close to the instantaneous rate of change of  $x$ . Therefore,

$$\frac{dx}{dt} \approx \frac{\Delta x}{\Delta t}.$$

We can now discretize the equation (2) by replacing  $dx/dt$  by  $\Delta x / \Delta t$ . Now we have

$$\frac{\Delta x}{\Delta t} \approx f(t, x). \quad (4)$$

Instead of a differential equation, we have a difference equation. In our previous example, we collected data on a population by month, so we would have already collected data. We would have values for the population at time points  $x_0, x_1, x_2$ , and so on. However, if we did not have data collected, we could use the ordinary differential equation to model a population. In that case, we would want to numerically estimate each  $x_n$  by using Euler's method which can be used for solving ordinary differential equations [8].

Euler's method begins with  $t_0$  and the corresponding  $x_0$ , the ordinary differential equation (2), and the change in time  $\Delta t$  and uses these terms to find the number in a population after one  $\Delta t$  has occurred. We can call this population  $x_1$ . Then we can use the new point  $x_1$  as well as the rate function (2) and  $\Delta t$  to find the next point  $x_2$ . We can continue this process until we have collected estimated population at times  $t_1$  through  $t_n$ . We can then use these  $x_n$  points to solve for the change in the population  $\Delta x$ . We can use (4) to solve for  $\Delta x$  starting from a specific time  $t_n$  and thingy  $x_n$ . We find

$$\Delta x \approx \Delta t \cdot f(t_n, x_n). \quad (5)$$

As we move from time  $t_n$  to  $t_{n+1}$ , our corresponding change in the population  $\Delta x$  is given by

$$\Delta x = x_{n+1} - x_n.$$

We can substitute in equation (2) to equation (5). Then we can solve for  $x_{n+1}$ :

$$x_{n+1} \approx x_n + f(t_n, x_n)\Delta t.$$

This allows us to iteratively estimate the solution of our ordinary differential equation.

## 2.1 Vector-valued functions

We will now look at the same differential equation, except the function  $x$  is vector-valued. We would use this form when we have a system of ordinary differential equations. An example would be  $\vec{x}(t) = (x(t), y(t), z(t))$ . First we know that  $\Delta\vec{x}_n = \vec{x}_{n+1} - \vec{x}_n$  and  $\Delta t_n = t_{n+1} - t_n$  because we can use change in time  $\Delta t$  to get from  $\vec{x}_n$  to  $\vec{x}_{n+1}$ . We can write our ordinary differential equation as

$$\frac{\partial\vec{x}}{\partial t} = \vec{f}(t, \vec{x}).$$

Recall that as  $\Delta t$  gets smaller the average rate of change of  $\vec{x}$  gets closer to the instantaneous rate of change of  $\vec{x}$ . We also know that  $\frac{\partial\vec{x}}{\partial t}$  represents the derivative with respect to time. Therefore, when  $t$  is small,

$$\frac{\Delta\vec{x}_n}{\Delta t_n} \approx \frac{\partial\vec{x}}{\partial t}.$$

Then, going through this same process as before, we obtain

$$\vec{x}_{n+1} \approx \vec{x}_n + \vec{f}(t, \vec{x})\Delta t.$$

The preceding equation is again Euler's method because each of the parts of the equation are the same, but they are vector valued [8]. Treating  $x$  as a vector part sets up a categorical system for each age or size category.

## 3 The McKendrick-von Foerster equation

First we will interpret the McKendrick-von Foerster equation (1). We rearrange this equation to this form:

$$\frac{\partial n}{\partial t} = -\frac{\partial n}{\partial a} - m(a)n,$$

Let's look at the population  $n$  at a specific time  $t^*$  and age  $a^*$ . Then  $\partial n/\partial a$  is the net change in population due to individuals aging out of the population with age  $a^*$  and the individuals that are aging into the population with age  $a^*$ . Also,  $m(a^*)n$  is the percent of individuals of age  $a^*$  who die. The net change in population over time is the term  $\partial n/\partial t$ . The McKendrick-von Foerster equation determines this rate of change population based on the changes due to the other two factors.

For the McKendrick-von Foerster equation, the variable for time gets discretized into time intervals of length  $\Delta t$  and the variable for the age variable gets sorted into categories by age. We saw how time gets discretized in Section 2. Now we will look at age. For instance, the variable for age could be set up as a matrix containing a set of variables  $a_m(t)$  where  $a$  represents age,  $m = 0, 1, 2, 3, \dots$  and  $t$  represents time. In this case, age category 0,  $a_0$ , would represent individuals ages 0 to 1. Similarly, age  $a_m$  represents the individuals ages  $m$  to  $m + 1$ . This is exactly described above, but with  $a_m(t) = \vec{x}_n$ .

Now we can combine what we have learned about discretizing ordinary differential equations and the McKendrick-von Foerster equation to look at the discretization of the McKendrick-von Foerster equation. Since McKendrick-von Foerster equation is a partial differential equation, we can discretize a variation of this model in order to create the general matrix model [10]. Discretization of time  $t$  transfers the variable from a continuous variable to a discrete variable; time is then defined by incremented changes in time.

### 3.1 Discretization of the McKendrick-von Foerster equation

The next step is to discretize the equation with respect to both variables and interpret. Recall that  $\Delta t$  is a discrete time increment and  $\Delta a$  as the corresponding age category change for our  $\Delta t$ . We have seen how we can use  $\Delta t$  to get points  $t_{n+1}$  using  $t_n$  by equation (3). Now we can look at the age variable  $a$ .

Before we go into discretizing age, we will talk about the difference between interpreting discretized age and discretized time. Discretized time can be thought of as points in time. Each  $t_n$  represents a point in time that has passed since the individual was last observed. As we talked about before, we can get from any  $t_n$  to  $t_{n+1}$  using  $\Delta t$  (3). In this case,  $\Delta t$  represents the amount of time that has passed since a subject has been studied. Discretized age is different. The  $\Delta a$  we look at is the width of an age category, but the age categories themselves are represented as  $a_k$  with  $k = 0, 1, 2, 3, \dots, k$  giving a number to each category. These  $a_k$  are not points, but groups of individuals which fit in the  $k^{\text{th}}$  age category. The change in age  $\Delta a$  is not an incremental change of a time unit. We are looking at age categories containing individuals from an age range of  $\Delta a$ . We still represent this as

$$a_{k+1} = a_k + \Delta a$$

where  $a$  represents age category and  $k$  represents the  $k^{\text{th}}$  age category. Notice that this is exactly the same as the relationship between  $t_n$  and  $t_{n+1}$  (3). Say that  $\Delta a$  is 1 year. Then we can start at the first category of ages, which includes all individuals who are under 1 years old; call it  $a_0$ . The next age category includes all individuals between 1 and 2 years old. Let's call this category  $a_1$ ; notice that  $a_1 = a_0 + \Delta a$ . We can continue this process and get each age category. This addition of  $\Delta a$  strictly means the age category 0,  $n(a_0)$  includes all individuals ages 0 to 1 years old. Then for example,  $a_5$  would be one year older than the previous age group; call it  $a_4$ . The distance between those two groups is 1 year since  $a_5 = a_4 + \Delta a$ . And we can also compare  $a_5$  to each of the previous points. For example, the distance from  $a_0$  to  $a_5$  is 5 years. Therefore, at  $n(t, a_5)$ , we are looking at individuals who are 5 years old at time  $t$ .

We can now use the previous information about  $\Delta t$  and  $\Delta a$  to look at a population based on discretized time and age variables. First we will discretize time. A time discretized population at time  $t$  and age  $a$  with  $r$  size categories,  $n(t, a)$ , can be thought of as  $\vec{n}(t)$  defined as

$$\vec{n}(t) = \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \\ \dots \\ n_r(t) \end{pmatrix},$$

which represents the population at time  $t$  for population ages [9]. For example, the population  $n_1(t)$  represents the number of individuals in a population that are age 1 at any give time  $t$ . Then the next population  $n_2(t)$  represents the number of individuals in a population that are age 2 at any given time. Each population in this matrix can be described in this way.

If we want to find populations of an age class  $a$  at discrete times, we simply use  $\Delta t$  to get from one time increment to the next. Say we start at  $t_0$  and we want to get to another time  $t$  We can add  $\Delta t$  to do that as have done before.

We will now take  $n(t + \Delta t, a + \Delta a)$  and discretize age using the subscript  $k$  to denote age classes. In this case, we want to move from age class to age class, so we will need a change in population age  $\Delta a$  which we will call  $\vec{n}_{k+1}$ . We want to know the the population for age class  $k$  from one time to the next time point  $\Delta t$ . Therefore, we can use the components of (1). We can now define the change in population age  $k + 1$  at time  $\Delta t$  as

$$\vec{n}_{k+1} = n_k(t)(1 - m(a_k)\Delta t),$$

where  $a_k$  denotes the  $k^{\text{th}}$  age class. This means that we are taking the population of size class  $k$  at time  $t$  times the percent of individuals in size class  $k$  that died at time  $t$  for a given change in time  $\Delta t$ .

Now we can look at the McKendrick-von Foerster equation with time  $t$  and age  $a$  discretized. Starting at time  $t$  with age category group  $a$ , the change in population age over the time interval  $\Delta t$  and its corresponding change in age category  $\Delta a$  is given by

$$n(t + \Delta t, a + \Delta a) = n(t, a)(1 - m(a))\Delta t,$$

where  $1 - m(a)$  is the percent of an age group  $a$  that did not die in time  $\Delta t$  [9]. This equation includes both  $\Delta t$  and  $\Delta a$  to chart a group of individuals of age  $a$  over all times with change in time equal to  $\Delta t$ . We made similar changes to the model in the study, but instead of the variable  $a$  representing age, the model made by Xia and Yamakawa uses class sizes to chart changes in the population over time.

### 3.2 Understanding Xia and Yamakawa’s process of discretizing the McKendrick-von Foerster Equation

Now that we have looked at the discretization of the McKendrick-von Foerster equation, we can look at how Xia and Yamakawa discretized the McKendrick-von Foerster equation. First, we must understand the difference between size class and age class. These two variables are similar in implementation, but we interpret them differently.

Like we talked about previously, for age classes with  $\Delta a = 1$ , we observed that each  $a_n$  represented a group of ages making up an age class. For example,  $a_{10}$  includes all individuals ages 10 to 11. Age classes are time specific and correlate with time very closely. This is because the age of a person depends on time. However, size categories are a group of individuals. They do not represent a person of a specific age, but a group of sizes. That specification can be different from model to model. For example, it could be represented in “metamorphosis stages” of a butterfly: egg, larva (caterpillar), pupa (chrysalis), and adult (butterfly).

For size classes, the growth is in the size and size doesn’t necessarily depend on time the same way as age. Each class represents individuals corresponding that a specific size. This becomes a bit more complicated because changes in size are due to more than just an individual growing up and their mass getting larger. For our butterfly example, the size classes could be separated into the four stages as done above. We could also separated further and track growth within each of these stages as well. For example, there could be three different sizes in the larva stage and one larger size in the pupa stage.

For the model in the Xia and Yamakawa paper, the size classes are even more complicated than the butterfly example. These individuals can grow in size and shrink in size. Growing in size could also be due to eating another individual, getting pregnant, or other non-adolescent growth reasons. Some examples of shrinking could be from getting eaten by another fish, digesting food, and being pregnant and then expelling the newborns. Also, the population  $n_i(t)$  is measured as individuals per meter cubed, which represents a population density, to accommodate for the vastness of the ocean.

Xia and Yamakawa give details on how they discretized the McKendrick-von Foerster equation, and how they adapted the equation for their model [10, Appendix S1]. They need to represent both individuals who are growing and individuals who are shrinking (e.g. due to digesting food, giving birth). To do so, they define  $g_i$  as the assimilation rate of an individual’s body breaking down, absorbing, and transforming nutrients into energy the body can use. This energy is classified in two categories: energy the body can use and energy the body cannot use. Energy that can be used travels through the body to the places it is needed. Energy that cannot be used is removed from the body in the form of excrement. They define the difference in mass between the class size  $i$  and  $i + 1$  as  $\Delta m_i = m_{i+1} - m_i$ . Since marine life cannot live forever, they also include an overall rate of mortality which they define as  $\mu_i$ . Then  $G_i$  counts the number of individuals who grow from size class  $i$  to  $i + 1$ .

For the individuals that shrink, they define variable counterparts to the growing variables. Note that this could be because of many different reasons such as getting eaten by another fish, expelling a new born/eggs at the end of pregnancy, or digesting food to make energy; we are also treating a fish getting eaten as shrinking, but it is actually decreasing the amount of fish in a size class. Xia and Yamakawa use a variable called  $F_i$  to represent the rate at which individuals move from size class  $i + 1$  to size class  $i$ . Recall that  $g_i$  is the rate at which individuals move from size category  $i$  to  $i + 1$ . Then the rate  $F_i$  is comparative to  $g_i$ ; they are counterparts to one another. Now, we can represent the number of individuals who move from size class  $i + 1$  to size class  $i$  by  $B_i$ .

It is also important to understand that when fish die for reasons other than predation and fishing, their



body mass moves to the  $m(0)$  class immediately. This means they can move from any size category  $i$  to size category  $i = 1$ . This component is also wrapped in the “shrinking” of an individuals. The population of the first size category  $n_1(t)$  is made up of several components including the excrement from metabolism, left over sperm and unborn individuals from reproduction, and individuals which have died. In this system, a recycling process prevents mass from leaving the system. Recycling of individuals means that there is a fixed amount of mass in the system that stays constant over time. This means that as  $t$  gets larger, the total of all of the mass will continue to be the same amount; no mass is lost in this system.

Now that all of the parts are represented, we have to piece them together. Starting with the number of individuals who are growing from size class  $i$  to size class  $i + 1$ , we need get the population who grew from one class to another using the population  $n_i(t)$  as well as the rate at which the population grows from one size class a size class larger,  $g_i$ . We want this population times this rate divided by the differences between the two masses,  $\Delta m_i = m_{i+1} - m_i$ . Then we get the number of individuals who grew from size class  $i$  to size class  $i + 1$ . Similarly for the shrinking size classes, we want the number of individuals in the population  $n_i(t)$  times the number of individuals which go from size class  $i$  to size class  $i - 1$ . Then we want to divide this product by the differences between the two masses,  $\Delta m_i = m_{i+1} - m_i$ . Then we get the number of individuals who shrink from size class  $i$  to size class  $i - 1$ . Now we can define both  $G_i$  and  $B_i$  to be

$$G_i := \frac{g_i n_i}{m_{i+1} - m_i}$$

$$B_i := \frac{F_i n_i}{m_{i+1} - m_i}$$

where  $G_i$  is the number of individuals growing into size class  $i + 1$  and  $B_i$  is the number of individuals shrinking to size class  $i - 1$ .

We can now take the previous variables and structured them into a form like the McKendrick-von Foerster equation (1) by making the following differencing scheme:

$$\frac{n_i(t + \Delta t) - n_i(t)}{\Delta t} = -\frac{g_i n_i(t) - g_{i-1} n_{i-1}(t)}{\Delta m_i} - \mu_i n_i(t), \quad i > 2, \quad (6)$$

To see the similarities between the McKendrick-von Foerster equation (1) and the equation (6), we can piece the differencing scheme equation (6) back together. Recall from our discretization section that

$$\frac{\partial n}{\partial t} \approx \frac{n_i(t + \Delta t) - n_i(t)}{\Delta t}.$$

This is exactly what we have on the left-hand-side of the equation (6). For the right-hand-side, recall that  $g_i$  is the rate at which the population grows from from size class  $i$  to size class  $i + 1$ , and  $g_{i-1}$  is the population rate growing from size class  $i - 1$  to  $i$ ; the  $\Delta m$  is the difference between the masses of individuals is size class  $i$  and size class  $i + 1$ . Here we can think of  $g_i \cdot n_i(t)$  as the number of individuals remain in size category  $i$  and  $g_{i-1} \cdot n_{i-1}(t)$  as the number of individuals who remained in size category  $i - 1$ . This is effectively the number of individuals in size category  $i$  minus the individuals in size category  $i - 1$ , which we can write as  $\Delta a := n_i(t) - n_{i-1}(t)$ . Then we have

$$\frac{\partial n}{\partial a} \approx \frac{n_i(t + \Delta t) - n_i(t)}{\Delta a} \approx \frac{g_i n_i(t) - g_{i-1} n_{i-1}(t)}{\Delta m}.$$

The last part of equation (1) is  $-m(a) \cdot n(t)$ . Recall that  $m(a)$  is the death function and  $n(t)$  is the population at time  $t$ . We will look at  $-\mu_i n_i(t)$  in equation (6). Xia and Yamakawa defined  $\mu_i$  as the total mortality rate, and we know that  $n_i(t)$  is the population in size category  $i$  at any time  $t$  [10]. Therefore, the function  $-\mu_i n_i(t) \approx -m(a) \cdot n(t)$ .

We can rewrite the equation (6) by moving the population based on age component with the population based on time component:

$$\frac{n_i(t + \Delta t) - n_i(t)}{\Delta t} + \frac{g_i n_i(t) - g_{i-1} n_{i-1}(t)}{\Delta m_i} = -\mu_i n_i(t), \quad i > 2. \quad (7)$$

We can see that this model has a similar components to the McKendrick-von Foerster equation (1).

Though equation (7) is describing size classes and the McKendrick-von Foerster equation is describing age, these variables are working in a similar manner. Also, both age and size can be used to chart the growth of a population over time.

Equation (7) accounts for the movements from size class to size class for the reproduction variable and the metabolism variable. More specifically, the increases in size include becoming pregnant, eating, and other actions of that nature. The decreases in size include releasing newborns, metabolizing food, and other actions of that nature. In the metabolism variable, energy is being taken in whereas in the reproduction variable, energy is being used. Also, note that there is only so much energy an organism can intake and expend at a given time.

## 4 Model

Xia and Yamakawa [10] studied the new, discretized equation which I describe as a general matrix model. This model is more complicated than the McKendrick-von Foerster equation because there are several parts in which the relationship between size categories and the marine population are intertwined. The population  $n(t)$  is the community structure defined as the column vector

$$n(t) = \begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ \dots \\ n_r(t) \end{pmatrix}. \quad (8)$$

This community structure accounts for the number of organisms in each size category. The first population  $n_1(t)$  is the population of the smallest size class, consisting of dead organisms, semen, and other particles. Waste from all size categories larger than  $n_1(t)$  is recycled into back into  $n_1(t)$ . Therefore,  $n_1(t)$  is acting as a recycling category which conserves mass in the system. The next population,  $n_2(t)$ , gives the population of the next smallest size class. Size category two is the smallest size category of living beings, including eggs and embryos. This continues for the next  $r$  size classes.

The model then bases the change in population over time using net changes of the variables predator-prey interaction, metabolism, reproduction, and fishing plus other non-predator-prey factors. The net change in the population of each size category from the predator-prey relationship is represented by the term  $\Delta n^P$ . The net change in the population of each size category from reproduction is represented by the term  $\Delta n^R$ . The net change in the population of each size category from metabolism is represented by the term  $\Delta n^Q$ . Lastly, the net change in the population of each size category due to non-predatory and fishing deaths is represented by the term  $\Delta n^U$ . The preceding variable includes, but is not limited to, disease and competition.

Adding the community structure and all of the net changes together gives us the density of marine life in each size category at a specific time  $t$ . Thus the community matrix model is defined as

$$n(t + \Delta t) = n(t) + \Delta n^P + \Delta n^R + \Delta n^Q + \Delta n^U, \quad (9)$$

where  $t$  represents a change in time. This equation is the completed model we will use to chart the changes of marine communities. Each of the delta variables in equation (9) will be discussed after providing a zoomed

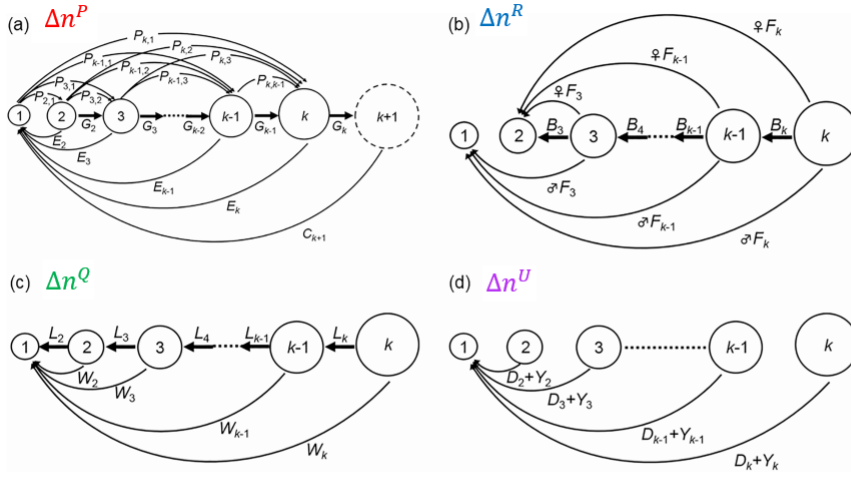


Figure 1: Figure 1 from [10] denoting a pictorial interpretation of the net changes between size classes within the model. In the graphic,  $\Delta n^P$  is the net change in population from predation,  $\Delta n^R$  is the net change in population from reproduction,  $\Delta n^Q$  is the net change in population from metabolism, and  $\Delta n^U$  is the net change in population from fishing and other non-predation deaths.

in look at one of the deltas. The figure below gives a breakdown of how the model is handling each of the delta variables.

Now we zoom into one of the deltas:  $\Delta n^P$ . Each of the deltas in (9) can be broken up into smaller parts. For example,  $\Delta n^P$  is explained in three parts: the total number of prey in a specific class size that was eaten by predators ( $-\Delta n^{Pminp}$ ), the change in the number of animals due to growth and recycled dead flesh ( $\Delta n^G$ ), and the increase in resources from recycling the undigested materials at a specific delta time unit ( $\Delta n^E$ ). Note that the the resources that are recycled in  $\Delta n^E$  are added to size category 1. Adding these variables together is the change in population size due to the predator-prey relationship, which is defined as

$$\Delta n^P = -\Delta n^{Pminp} + \Delta n^G + \Delta n^E. \quad (10)$$

However, we can zoom in even farther because  $-\Delta n^{Pminp}$ ,  $\Delta n^G$ , and  $\Delta n^E$  can be broken down into a mixture of vectors and matrices. Note that we will be representing the model using 4 size categories for simplicity. For example,  $\Delta n^E$  is defined as

$$\Delta n^E = T_1 M_1^{-1} (I - E) N V S M \cdot n \cdot \Delta t, \quad (11)$$

where  $T_1$  is a transformation matrix defined by

$$T_1 = \begin{pmatrix} 1 & 1 & 1 & 1 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}.$$

This matrix moves the waste from each size category into size category 1: the waste size category. The matrix  $M_1$  includes the value  $m_1 = 0.001 \cdot 10^{-1} = 0.0001$  on the main diagonal defined as

$$M_1 = \begin{pmatrix} m_1 & 0 & 0 & 0 \\ 0 & m_1 & 0 & 0 \\ 0 & 0 & m_1 & 0 \\ 0 & 0 & 0 & m_1 \end{pmatrix},$$

where  $m_1 = 0.0001$  is the prey body mass of size class 1. When used in  $\Delta n^E$ , the inverse of this matrix converts the mass of all of the individuals into the number of individuals in each size category. The matrix  $I$  represents the  $4 \times 4$  identity matrix. Matrix  $E$  represents the assimilation of predators in each class size defined by

$$E = \begin{pmatrix} e_1 & 0 & 0 & 0 \\ 0 & e_2 & 0 & 0 \\ 0 & 0 & e_3 & 0 \\ 0 & 0 & 0 & e_4 \end{pmatrix},$$

where  $e_1, e_2, e_3,$  and  $e_4$  represent the amount of marine life digested in predators of each class size. In our  $\Delta n^E$ , the subtraction of  $E$  from  $I$  is calculating the mass in each size category which is moved by matrix  $T_1$  to size category 1. This is representing the left over mass of prey that predators have eaten. Matrix  $N$  is defined by

$$N = \begin{pmatrix} n_1(t) & 0 & 0 & 0 \\ 0 & n_2(t) & 0 & 0 \\ 0 & 0 & n_3(t) & 0 \\ 0 & 0 & 0 & n_4(t) \end{pmatrix},$$

which represents the number of prey in each class size and  $n$  represents the number of prey in each of the size classes. The matrix  $V$  is defined as

$$V = \begin{pmatrix} \gamma \cdot m_1^p & 0 & 0 & 0 \\ 0 & \gamma \cdot m_2^p & 0 & 0 \\ 0 & 0 & \gamma \cdot m_3^p & 0 \\ 0 & 0 & 0 & \gamma \cdot m_4^p \end{pmatrix},$$

where  $\gamma$  is the factor for searching rate equal to  $600m^{-3}yr^{-1}g^{-p}$ , and  $m$  represents the body mass index for class size 1 to 4 to the searching rate  $p = 0.75$ . The matrix  $S$  is a size selectivity matrix of a predator of class  $i$  on a prey of class  $j$ .  $S$  is defined as

$$S = \begin{pmatrix} 0 & 0 & 0 & 0 \\ \phi_{2,1} & 0 & 0 & 0 \\ \phi_{3,1} & \phi_{3,2} & 0 & 0 \\ \phi_{4,1} & \phi_{4,2} & \phi_{4,3} & 0 \end{pmatrix},$$

where  $\phi_{i,j}$  is a piece-wise function of body mass ratio between predator and their prey. This function is defined as

$$\phi_{i,j} = \begin{cases} \exp\left(\frac{-\left(\log\left(\frac{\beta_i m_j}{m_i}\right)\right)^2}{2\sigma^2}\right) & \text{if } j > 1 \\ \left(\sum_{x=-s}^1 \exp\left(\frac{-\left(\log\left(\frac{\beta_i m_x}{m_i}\right)\right)^2}{2\sigma^2}\right)\right) & \text{if } j = 1 \end{cases},$$

where  $\phi_{i,j}$  makes sure that predators prefer prey smaller than them. The parameter  $\beta$  represents the most desired prey size for a predator of some size class  $i$ ,  $\sigma$  represents the range of prey size classes that predators

would want to consume, and  $m_i$  is still the body mass index of a predator of size class  $i$ . Note that this model is assuming that predators eat prey in size categories smaller than their own based around the idea that predators prefer to hunt and kill smaller prey [7, 10]. Also, note that this model assumes that predators are not preying on prey in the same size category as themselves. The last matrix is matrix  $M$  defined as

$$M = \begin{pmatrix} m_1 & 0 & 0 & 0 \\ 0 & m_2 & 0 & 0 \\ 0 & 0 & m_3 & 0 \\ 0 & 0 & 0 & m_4 \end{pmatrix},$$

where each  $m_c$  represents the body mass of prey for class size 1 through 4. Though each of the quantities  $\Delta n^P$ ,  $\Delta n^R$ ,  $\Delta n^Q$ , and  $\Delta n^U$  can be broken up this way, we will focus on the equations for each of the quantities previously mentioned, what the delta's in their equations mean, and why they are represented as such.

Continuing with the predation term,  $\Delta n^P$ , predation is a large component to marine life. This system includes each kind of animal, the animals they eat, and the animals that hunt them. The predator-prey relationship is important to include when studying the changes in a marine population because that accounts for the growth, decline, and survival of a population as well as the health of the community as a whole.

Next we will talk about the term  $\Delta n^R$ , which represents the reproductive element of this system. This system includes marine individuals being born, the death of under developed/unborn individuals, the eggs or embryos of each individual, and the sperm of each individual.

Including the reproductive element is important for two reasons. Firstly, reproduction replenishes the population when it experiences death. It is also the only element which grows a population. Secondly, in this case it is assumed that the leftover waste from reproduction, whether that be leftover/expelled sperm or unborn embryo, is recycled back into the system to be used as fuel for larger size categories. More on this will be discussed later when we talk about the recycling variable. The reproductive variable counts the number of newborn marine life and changes each size category accordingly. We define the reproductive variable as

$$\Delta n^R = \Delta n^F + \Delta n^B, \tag{12}$$

where  $\Delta n^F$  represents the amount of semen added to size category 1, and the number of eggs added to size category 2. The other part,  $\Delta n^B$ , denotes the shifts from size category to size category once an individual has given birth. This delta  $\Delta n^R$  accounts for the each part of reproduction: the birth of new marine life and the shift in size class due to the increase in newborns, as well as the shift in size class of the individuals once they have given birth.

Another term in the community matrix model is the metabolism term  $\Delta n^Q$ . This encompasses the digestion of food, the excrement that the animal leaves behind, and the process of turning food into energy from that digestion. This variable is defined as

$$\Delta n^Q = \Delta n^W + \Delta n^L, \tag{13}$$

where  $\Delta n^W$  represents when metabolites are recycled into size category 1 as a result of the consumers metabolising food for energy and  $\Delta n^L$  represents the decrease by one size class for the marine life that undergoes this process: the consumers. This process is about making energy and excrement from digestion. In this case, the consumer is considered larger than those in size category 1.

The metabolism term is important to include because it is marine life eating other marine life. Therefore, marine life that are accounted for growing are also being eaten. Once they are eaten, they are digested, and their mass becomes either energy or excrement. In this case, the eaten individual does not reduce in size, but its mass is added to the first size class. Therefore, the process of growth, recycling, and death make this variable helpful in discussing population of marine life. It also ties in to the other deltas making up (9). Lastly, this system is a non-waste system, meaning everything gets recycled back into the system. The

metabolism term accounts for the moving of mass around in the system so that the system is conserving mass, and accounts specifically for the recycling of waste through excrement.

The last term in (9) is  $\Delta n^U$  which denotes the change in population size depending on other outside factors. This term is somewhat of an umbrella term for all other deaths besides deaths from predation. Examples include fishing, disease, and death from old age. This non-predation variable is defined as

$$\Delta n^U = -\Delta n^{D-\text{loss}} + \Delta n^{D-\text{recycle}} - \Delta n^{Y-\text{remove}} + \Delta n^{Y-\text{recycle}}, \quad (14)$$

where  $-\Delta n^{D-\text{loss}}$  is removing the mass that died from each size category,  $\Delta n^{D-\text{recycle}}$  takes the mass removed from each size category and recycles it back into the system from those non-predation deaths,  $\Delta n^{Y-\text{remove}}$  accounts for the mass lost from human fishing, and  $\Delta n^{Y-\text{recycle}}$  recycles the mass lost from human fishing back into size category 1. This term is particularly important to include since this accounts for the deaths in a marine population due to survival of diseases and other unforeseen threats in a population. Also, notice that  $\Delta n^{D-\text{recycle}}$  and  $\Delta n^{Y-\text{recycle}}$  are conserving mass within the model lost from fishing and non-predation deaths.

This death term must be included because it accounts for death from what can be considered “natural” causes. The death of fish due to disease, old age, or other non-predation related deaths affects the population constantly. This variable is vital in describing the population of marine life. For example, we could this of a population of humans. Much like marine life, we also take on deaths in the human population due to non-predatory reasons. In many cases for humans, deaths are non-predatory related.

## 5 Implementing the mini model

Xia and Yamakawa developed a size structured matrix model with  $k$  size categories. To study the results of the model, they chose  $k = 50$  size categories [10]. We chose  $k = 10$  size categories to simplify the model further for study.

In order to study Xia and Yamakawa’s population model, we made a mini version of the model in Mathematica. We first set parameters we would need for our matrices [10]. Then we began building the model by parts. We first build the net changes in the population due to predation. We define all the matrices necessary for the equation (10) using tables, piecewise functions, and commands such as `DiagonalMatrix`. We constructed all of the deltas within (10). Finally, we constructed our  $\Delta n^P$ . We then followed this process, starting with building the matrices, for each of the remaining net changes:  $\Delta n^R$ ,  $\Delta n^Q$ , and  $\Delta n^U$ . Once we had all of these net changes, we made our community matrix (8). We then defined our function  $n(t + \Delta t)$  recursively, taking care that Mathematica could remember output once computed, and began studying our mini model. We discuss some of the challenges later on.

In this study we chose  $k = 10$  size categories. Recall that the first size category is the waste class, so we are looking at the waste class and nine classes consisting of living beings. We then used the model to better understand how the mini model was behaving.

### 5.1 Challenges We Faced While Interpreting Results

When first implementing the mini model, we started with  $k = 4$  size categories. We expected to see the populations of each size category stabilize at a certain positive number of individuals per meter cubed. However, we saw extinction in most of the size categories. We then looked in the code for errors. After looking through the code, we wondered how increasing the number of size categories might affect the results we saw. We increased the number of size categories to 10. When we had 10 size categories, we saw that the population did not decrease as suddenly. However, the population would continue to eventually go extinct. Since we saw that the population did not go extinct as quickly with 10 size categories, we noticed that adding size categories was countering the time until extinction for each size category.

The next area we checked was the conservation of mass. Since this model conserves mass by recycling mass back into size category 1, adding the populations of each size category at time point  $t$  should be the same as at time  $t + 1$ . When we tried this, we saw that the population was dying off and mass was not being conserved. We will get into more detail about this in Subsection 5.3. Because of this, we check the construction of the model for where recycling occurred. When we found no errors in the construction of the model, we searched for errata. However, we did not find any errata. Once we had gone through all of these steps, we reached out to Xia and Yamakawa. We found out that the parameter  $\delta$  had to be scaled to fit the number of size categories we chose. The parameter  $\delta$  is the ratio of mass when comparing predators to prey. We needed to choose a  $\delta$  so that predators have prey which are the predator's preferred prey size as determined by the  $\phi_{i,j}$  function (4). When we contacted Xia and Yamakawa, they explained that predators would prey off of prey 100 times smaller than their mass, so increasing  $\delta$  is necessary to counteract the decrease in number of size categories.

Once we were able to adjust the parameter  $\delta$  in our mini model, we no longer saw extinction in most of the size categories, and we were able to get some results about what is happening to the population of each size category within our mini model.

## 5.2 Results with Ten Size Categories

Once we had changed  $\delta = 10$ , we were able to interpret the populations over time and look at how the mini model's results compared to Xia and Yamakawa's results [10].

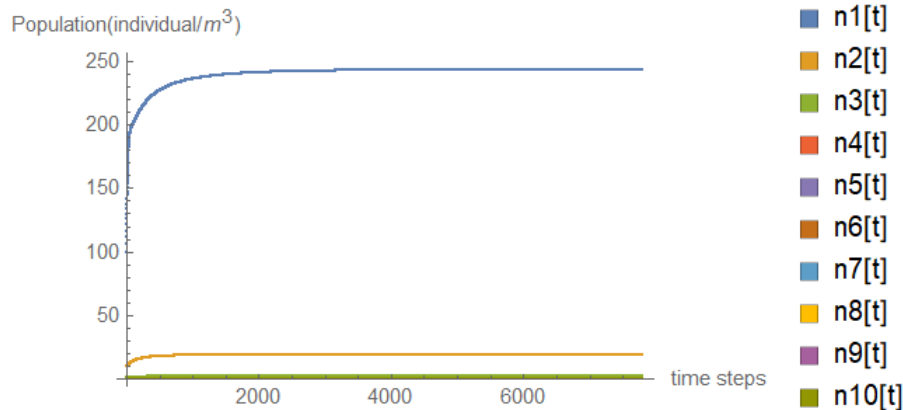


Figure 2: Density of individuals per meter cubed in the first three size categories over 40 years.

From Figure 2, we can see that as time increases, the populations of the first few size categories are evening out to a steady positive population. However, not all of the populations within this model can maintain a steady positive population. If we continue looking at some of the other populations, we notice that some of the larger size categories appear to be going extinct.

From Figure 3, we can see that the populations of size category six, seven, eight, nine, and ten all appear to be decreasing to zero as time goes on. This indicates extinction within our model. We tried significantly larger values of  $\delta$  and continued to see extinction in some of the larger size categories. This suggests that some of the other chosen parameters are not set at the best values for this model with 10 size categories. For example, we may need to change the time increment  $\Delta t$ , since that can play a role in how quickly predators find prey.

We also checked that our mini model was upholding the conservation of mass component of this model.

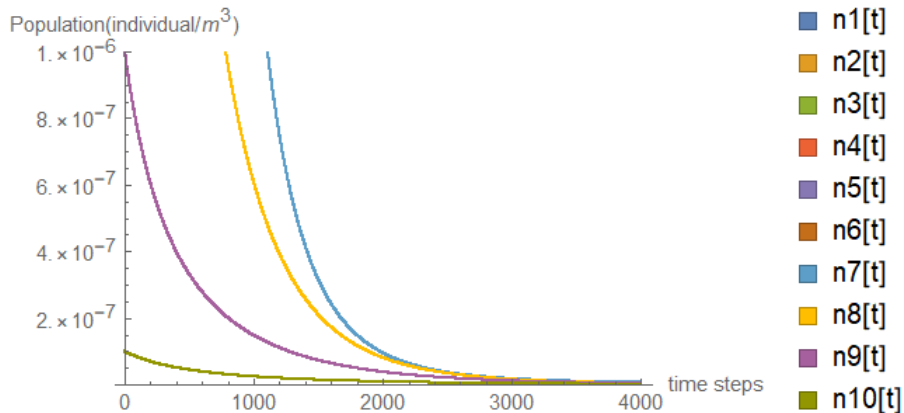


Figure 3: Density of individuals per meter cubed in the size categories 7, 8, 9, and 10 over 40 years.

In order to do this, we used the following equation to calculate the total mass density over time  $t$ :

$$m_1 n_1(t) + m_2 n_2(t) + m_3 n_3(t) + \dots + m_{10} n_{10}(t) = \text{Constant}, \quad (15)$$

where  $m_r$  is the mass of size category  $r$  and  $n_r(t)$  is the number of individuals in size category  $r$ .

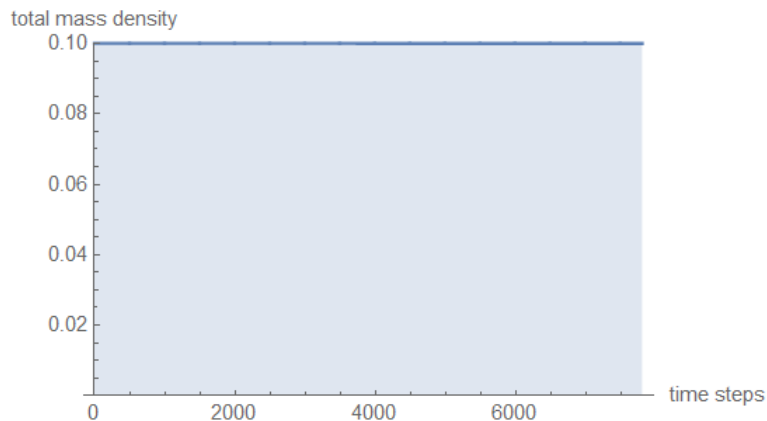


Figure 4: Total mass density in the mini model population remains constant over 40 years.

In Figure 4, we see that as  $t$  increases, the total mass is remaining constant. This means that mass is conserved within our mini model.

The conservation of mass was occurring in the mini model, but even with our improved  $\delta$ , we did not obtain long-term population behavior matching the real world. A good model should match this real-world population behavior, which is called the *empirical steady state*. From Xia and Yamakawa [10], the empirical steady state is

$$\log_{10}[\text{abundance}] = -0.9959 \cdot \log_{10}[\text{body mass}] - 2.006, \quad (16)$$

which is a regression line comparing the density of individuals per meter cubed to the mass of the individual. Xia and Yamakawa were able to achieve the steady state with  $\delta = 1.5$ ,  $k = 50$  size categories, and  $\Delta t = 0.001$ . In Figure 5, denoting the empirical steady state in orange and our model in blue, shows that our model does



not follow the steady state for larger individuals. This means that smaller size categories in our model are behaving as we would expect them to, but the population of larger size categories is smaller than we would expect. In some cases, the larger size categories are going extinct.

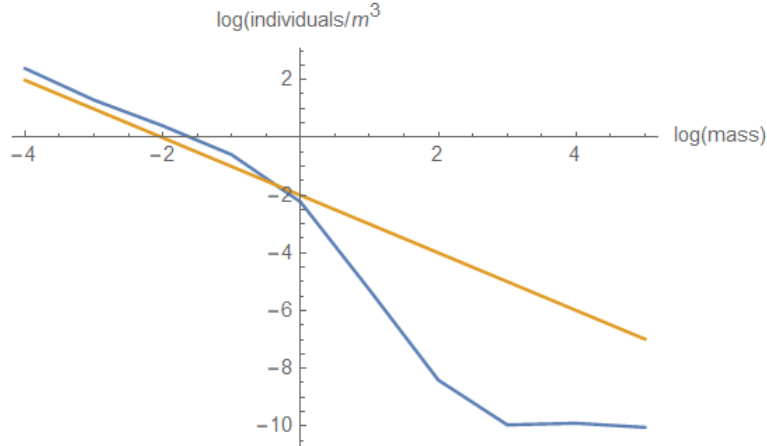


Figure 5: Comparison of the empirical steady state (orange line) and the relationship between population density and mass (blue line) in the mini model after 40 years. Note that we are close to the empirical steady state for small mass classes.

Since mass in our model was conserved, we can expect the extinction of some of the larger size categories is coming from insufficient increase in  $\delta$ , or another factor. However, the model is correctly recycling mass to the first size category.

## 6 Conclusion

In this paper, we studied a smaller version of Xia and Yamakawa’s population model [10]. Xia and Yamakawa used a variation of the McKendrick-von Foerster equation in order to make their model studying marine communities. Because of this set up, we went through what the McKendrick-von Foerster equation is: a differential equation which defines the population of a group in terms of age and time.

Since the McKendrick-von Foerster equation is the scaffolding of the Xia and Yamakawa’s model, we then discretized the McKendrick-von Foerster equation to better understand what is happening to the variables in the equation both mathematically and verbally. This is especially important when we talk about then transition between age categories and size categories. In order to understand the model, we also looked at an appendix to Xia and Yamakawa’s paper [10, Appendix S1], which contained information on how they discretized the metabolism variable and the reproduction variable. We built up that variation of the McKendrick-von Foerster equation involving the reproduction and metabolism variables [10].

After, we studied Xia and Yamakawa’s matrix model, which gave us the tools we needed to make a smaller version of the matrix model. We decided to make a mini matrix model with four size categories. This choice was made to simplify the model while continuing to understand how it works. Adjusting the parameter  $\delta$  fixed some of the issues we were seeing before. Once we scaled our model correctly, we were able to change parameters within the model and see how the ten size category, mini model results related to Xia and Yamakawa’s results.

The next step in this research of Xia and Yamakawa’s model would be to investigate the relationship between the number of size categories  $k$ , the  $\delta$  parameter, and our choice of  $\Delta t$ . We would want to find a

relationship between the number of size categories and  $\delta$  in order to get the empirical steady state immediately. We would also want to consider how that relationship relates to  $\Delta t$  because  $\Delta t$  needs to be small enough so that the population curve is smooth. Once we are able to get the relationship between  $\delta$  and a size category  $k$ , we could then purposefully change parameters in the model like Xia and Yamakawa have done in order to see how unbalancing parameters within the model affects the population over time. If we had more time, we could specifically change the fishing parameters to look at the effects on marine communities from unbalanced fishing.

# Appendix

Our Mathematica code for implementing the mini model is included as a supplement.

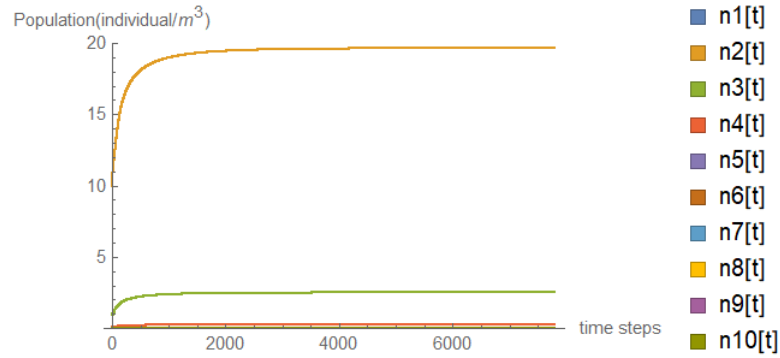


Figure 6: Density of individuals per meter cubed of size categories 2, 3, and 4 over 40 years.

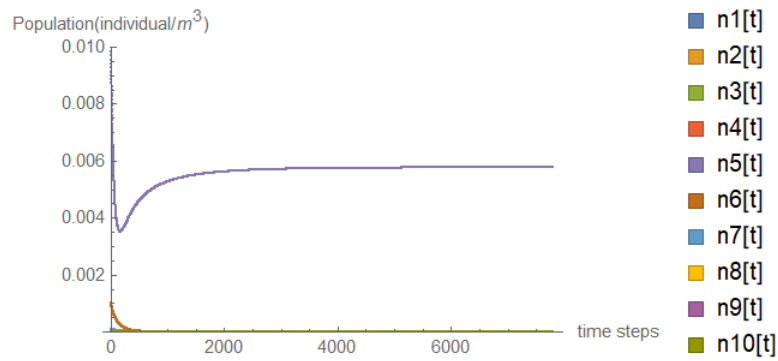


Figure 7: Density of individuals per meter cubed of size category 5 over 40 years.

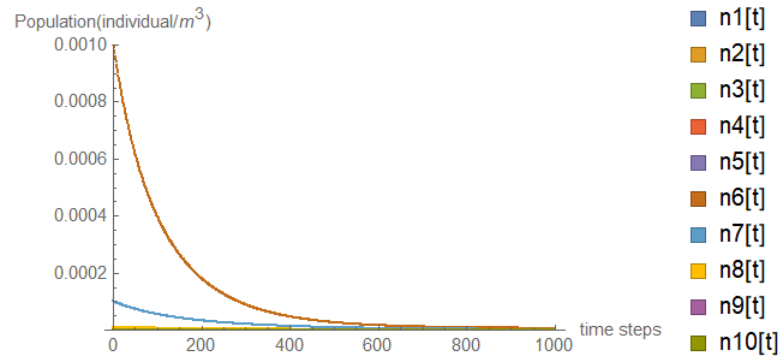


Figure 8: Density of individuals per meter cubed in size categories 6 and 7 over 40 years.

## **7 Acknowledgement**

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## References

- [1] Datta S, & Blanchard, J. L. The effects of seasonal processes on size spectrum dynamics. *Can J Fish Aquat Sci.* 2016; 73(4):598–610.
- [2] Keyfitz, B. L., & Keyfitz, N. The McKendrick partial differential equation and its uses in epidemiology and population study. 1997; *Mathematical and Computer Modelling*, 26(6), 1–9. Retrieved April 6, 2020 from <https://www.sciencedirect.com/science/article/pii/S0895717797001659>
- [3] Minkevich, I.G., Abramychyev, A.Yu. *The Rise and Decay of Cell Age Synchrony in the Model of Continuous Culture with McKendrick - Von Foerster Equation.* 1992; *IFAC Proceedings Volumes*, 25(2): 287-288. Retrieved August 18, 2020 from <https://www.sciencedirect.com/science/article/pii/S1474667017503730>
- [4] Maury, O., Shin, Y. J., Faugeras, B., Ben Ari, T., Marsac, F. Modeling environmental effects on the size-structured energy flow through marine ecosystems. Part 2: simulations. *Prog Oceanogr.* 2007b; 74(4):500–514.
- [5] Rojano, Fernando., Ibarra, Luis., Lira-Noriega, Andres., Escobar-Sarria, Federico., Gonzalez-Tokman, Daniel., Toledo, Porfirio., Tapia-Santos, Brenda., Hernández-Linares, Carlos. Application of a modified McKendrick-von Foerster equation to predict beetle population dynamics (*Xyleborus affinis*) under artificial medium in growth chambers. July 2018; Retrieved August 19, 2020.
- [6] Rossini, Luca., Speranza, Stefano., Contarini, Mario. Distributed Delay Model and Von Foerster’s equation: Different points of view to describe insects’ life cycles with chronological age and physiological time. *Ecological Informatics.* 2020; 59: 101117. Retrieved August 18, 2020.
- [7] Ursin E. On the prey size preferences of cod and <https://www.overleaf.com/project/5e8415bde8dc010001583503dab>. *Meddelelser fra Danmarks Fiskeri- og Havundersøgelser.* 1973; 7:85–98
- [8] (2020, July). Euler method. Wikipedia. Retrieved August 6, 2020, from [https://en.wikipedia.org/wiki/Euler\\_method#:~:text=In%20mathematics%20and%20computational%20science,with%20a%20given%20initial%20value](https://en.wikipedia.org/wiki/Euler_method#:~:text=In%20mathematics%20and%20computational%20science,with%20a%20given%20initial%20value).
- [9] (2020, February). Von Foerster equation. Wikipedia. Retrieved April 4, 2020, from [https://en.wikipedia.org/wiki/Von\\_Foerster\\_equation](https://en.wikipedia.org/wiki/Von_Foerster_equation)
- [10] Xia, S., & Yamakawa, T. A size-structured matrix model to simulate dynamics of marine community size spectrum. 2018; *PLOS ONE*, 13(6). Retrieved January 27, 2020, <https://doi.org/10.1371/journal.pone.0198415>