3-15-2021

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Recommended Citation

Panayotova, Iordanka N. and Hallare, Maila B. (2021) "Modeling the Ecological Dynamics of a Three-Species Fish Population in the Chesapeake Bay," *CODEE Journal*: Vol. 14, Article 2.
Available at: <https://scholarship.claremont.edu/codee/vol14/iss1/2>

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Modeling the Ecological Dynamics of a Three-Species Fish Population in the Chesapeake Bay

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Keywords: Mathematical modeling, fish population dynamics, prey, predator, invader

Manuscript received on May 17, 2020; published on March 15, 2021.

Abstract: We present an inquiry-based project that is designed for a mathematical modeling class of undergraduate junior or senior students. It discusses a three-species mathematical model that simulates the biological interactions among three important fish species in the Chesapeake Bay: the prey Atlantic menhaden and its two competing predators, the striped bass and the non-native blue catfish. The model also considers the following ecological issues related to these three species: the overfishing of menhaden, the invasiveness of the blue catfish, and the harvesting of blue catfish as a method to control the population. A series of modeling scenarios are considered based on some simplifying assumptions to demonstrate the application of theoretical concepts to actual fisheries in the Chesapeake Bay. Analysis involves elementary skills such as finding the roots of polynomial equations, computing eigenvalues and eigenvectors, and some advanced topics such as Routh-Hurwitz criteria and the Hartman-Grobman Theorem. Numerical simulations via MATLAB are utilized to produce graphical simulations and analyze long-time behaviors. Our model predicts that if no serious measures are taken to prevent the spread of the invasive blue catfish, the native predator species will be seriously affected and may even become extinct. The model also shows that linear harvesting is sufficient to limit the growth of the invasive catfish population; however, it is not sufficient to save the striped bass from becoming extinct. The results of this study illustrate the fundamental ecological principle of competitive exclusion, according to which two competing species that attempt to occupy the same niche in an ecosystem cannot co-exist indefinitely and one of the two populations will either go extinct or will adapt to fill a different niche.

1 Introduction

Chesapeake Bay, the largest estuary in the United States, is an extremely complex ecosystem. The fisheries of the Chesapeake Bay play a very important role in the ecosystem but have declined significantly as a result of habitat loss, deterioration in water quality, and the effects of the changing climate, only amplified by commercial over-fishing.¹

One particular example of a seriously affected native fish is the Atlantic Menhaden (*Brevoortia tyrannus*). Menhaden is important for both ecological and commercial reasons to the Atlantic region. Often called “the most important fish in the sea,” they are filter feeders that play an essential role in cleaning the water. They are also a critical link in the Chesapeake Bay food chain as they transfer nutrients from lower to higher trophic levels. The number of young menhaden in the Chesapeake Bay dropped dramatically in the early 1990s and still remains low.² On May 4, 2020, the Bay Journal announced:

The Virginia Marine Resources Commission unanimously adopted a new regulation that requires this year’s Bay menhaden harvest be cut by nearly half from what it was in 2019. Effective June 17, 2020, there will be a moratorium on fishing for menhaden in Virginia state waters. [8]

Another native fish that declined significantly is the striped bass (*Morone saxatilis*), a sought-after commercial and recreational catch and a key predator in the Bay food web. Menhaden is the main prey to the striped bass. Due to the decrease of Menhaden, some striped bass now struggle from poor nutrition, which is linked to a decrease in growth rates and an increase in sensitivity to disease.¹ Due to a critical decline of the bass, the Atlantic States Marine Fisheries Commission (ASMFC) has determined that conservation measures are needed for the 2020 fishing season. The Striped Bass Technical Committee and the ASMFC Board announced on February 4, 2020:

In addition to a cut in the commercial quota, targeting of striped bass by the recreational sector will be prohibited starting April 1 — including a prohibition of trolling — and the spring trophy season will be delayed until May 1. The department will also move forward with conservation options for the summer and fall seasons in the 2020 Implementation Plan. Measures in the summer and fall are designed to reduce mortality caused by high temperatures and low oxygen in the water.³

Another severe ecological impact on the native species in the Bay has been recently identified as a result of predation by invaders such as the blue catfish (*Ictalurus furcatus*). Brought to the region in the beginning of the 1970s for recreational purposes, the blue and flathead catfish now make up to 75 percent of total fish biomass in the Chesapeake Bay.⁴

¹<https://www.cbf.org/issues/fisheries/>, retrieved March 13, 2021

²<https://www.cbf.org/about-the-bay/more-than-just-the-bay/chesapeake-wildlife/menhaden/index.html>, retrieved March 13, 2021

³<https://www.proptalk.com/striped-bass-conservation-regulations-set-spring-2020>, retrieved March 13, 2021

⁴<https://www.fisheries.noaa.gov/feature-story/bay-invaders-blue-catfish-fishery>, published March 20, 2018, retrieved March 13, 2021

As novel apex predators that feed on important fishery resources, including native and anadromous fish, blue and flathead catfish have the potential to exert severe ecological harm to the region. Some preliminary studies have already documented harmful effects to native species; however, the full extent of negative impacts from catfish invasions remains poorly understood. In 2011, the Atlantic States Marine Fisheries Commission approved a resolution expressing concern about the impacts of blue and flathead catfish on Atlantic Coast migratory fish species. The resolution suggested that “all practicable efforts should be made to reduce the population levels and ranges of non-native invasive species” [2]. In 2018, the Fisheries News published by NOAA stated:

*The NOAA Chesapeake Bay Office (NCBO) and other Chesapeake Bay organizations identified invasive catfish as a challenge facing the Chesapeake ecosystem several years ago. The commercial and recreational fisheries are helping to control the population. NOAA Fisheries and our partners are supporting the development of these fisheries and working to identify further solutions to control the growth of this invasive population.*⁴

The Chesapeake Bay management jurisdiction tries to engage the public to minimize the ecological and economic effects of the catfish invasion by promoting harvesting. However, it is not clear if such a strategy will have any practical effects on the growing catfish population. Fisheries in the Bay are managed as single species entities, yet the multi-species nature of the ecosystem has to be taken into account when making management plans or taking management decisions about the Chesapeake Bay.

We create a three-species mathematical model to investigate the relationship between the three fish species in the Chesapeake Bay ecosystem: menhaden, striped bass, and catfish. We ignore interactions with other species, that is, we assume that there are no other predators, no other prey, and no other competitors. We also do not consider environmental or societal factors such as temperature, seasons, illegal fishing, etc. We use a system of ordinary differential equations and utilize linear stability theory, graphical analysis, and numerical simulations.

This inquiry-based project is developed for a Mathematical Modeling class with junior and senior undergraduate students. The model naturally builds upon the classic Lotka-Volterra equations for two interacting species, such as predator-prey interactions or two species competing for the same resources. Students are expected to have already taken linear algebra and differential equations. This project provides an opportunity to apply theoretical concepts to real-world problems related to fisheries in the Chesapeake Bay.

Using $x(t)$ to denote the prey population and $y(t)$ to denote the predator population over time t , the Lotka-Volterra predator-prey model introduces students to modeling the growth of two interacting populations:

$$\begin{cases} x' &= Ax - Bxy \\ y' &= -Dy + Cxy \end{cases}$$

where the parameters A, B, C, D are all positive. Each term in this system is a rate; in particular, the term Ax represents the linear growth rate of prey x , the term $-Bxy$ represents the predation rate of the predator y on the prey x during their interactions, the term $-Dy$

represents the rate at which the predator y will decrease without the prey as food, and the term Cxy represents the rate at which the predator y grows in the presence of the prey as food. When students understand the functional relationships between $x(t)$ and $y(t)$, they are able to build upon simple models such as these.

Although the Lotka-Volterra model is elementary and only uses basic knowledge of ecology, it may be used skillfully to encourage discussion and inquiry about theoretical ecology and real ecological issues. For example, the following guiding questions may inspire curiosity and help students reflect on the power of differential equations in modeling population dynamics:

1. What are the ecological assumptions in this model?
2. What happens to the prey population if the predator is absent, and vice-versa?
3. Does the predator rely only on the given prey for food and its existence? Does the model consider the various appetites of the predator and its competitors? What does the prey eat? Why do we assume that the rate of change of the prey population is proportional to its size?
4. How does the model consider the growth and death rates of the prey, the predator, and the competitor?
5. How does the model capture the strength of competition between competing predators? Will a stronger competition between predators benefit the prey?
6. Can we utilize the given model to any season, habitat condition, or environmental situation? How do we capture human, technology, and societal effects on the predator and prey populations?
7. How does one construct a model that considers a longer food chain and/or a more intricate food web?

In particular, the model that we present here builds upon the Lotka-Volterra model to analyze the dynamics and the ecological issues among the Atlantic menhaden (see Figure 1a), the striped bass (Figure 1b), and the blue catfish (Figure 1c). A schematic representation of the food web connection and the ecological issues considered in this project are given in Figure 2 and are explained in detail in the next section.

This paper is organized as follows. Section 2 presents the assumptions, variables, parameters, and differential equations that make up our mathematical model. It also contains preliminary analysis on the system's invariant sets. Section 3 investigates the three-species system with equal interference between two predators competing over one prey. This section records the computations for the equilibria and their stability analyses. It also presents a brief review of fundamental results in dynamical systems. Section 4 builds upon the system analyzed in Section 3 by considering harvesting scenarios. Section 5 continues to investigate the original system by varying the competition strength between the predators. Section 6 presents numerical simulations and analyses to support theoretical computations and to further uncover interesting behavior. Section 7 presents a list of

suggestions on how students may complete a report on their mathematical modelling project and a possible grading rubric. Section 8 restates the phenomenon being considered, summarizes the important mathematical results, and provides evidence-based answers to the ecological issues that motivated this study. Also, in many places throughout the paper, we include *Student Exploration Exercises* to supplement discussion and analysis in a mathematical modelling classroom.

2 Mathematical modeling of the fish dynamics

Let us analyze the biological interactions of a system that has two predators competing over one prey and two ecological concerns, namely, over-fishing of the menhaden and the invasion of the catfish on the Chesapeake Bay. Let $x = x(t)$ be the population of the Atlantic menhaden, $y = y(t)$ be the population of striped bass, and $z = z(t)$ be the population of blue catfish. We assume the following:

1. the prey x grows exponentially at a rate proportional to its size,
2. the two predators y and z are in competition, both preying on x ,
3. the predator y declines at a rate proportional to its size in the absence of x ,
4. the predator z is an invasive species and grows exponentially at a rate proportional to its size, and
5. the prey x and the predator z are harvested.

A. The most general system of differential equations describing the three-species biological interactions under the above assumptions is given by:

$$\begin{cases} x' &= ax - bxy - cxz - h_1x \\ y' &= -dy + bxy - \alpha yz \\ z' &= ez + cxz - \beta yz - h_2z. \end{cases} \quad (\text{A})$$

(a) Atlantic Menhaden, *Brevoortia tyrannus*, (a.k.a. Alewife, Bunker, Pogy, Bugmouth, Fat-Back)

(b) Striped Bass, *Morone saxatilis*, (a.k.a. Rockfish, Rock, Striper)

(c) Blue Catfish, *Ictalurus Furcatus*, (a.k.a. Hump-back blue)

Figure 1: The three fish species in Chesapeake Bay in this project, their scientific and common names. Pictures from Chesapeake Bay Program, www.chesapeakebay.net.

**Ecosystem Connection and Issues
Between the Three Fish Species**

Figure 2: The food web connection and ecological issues among the three fish species. The one-sided blue arrows represent predation towards prey; the red double-arrow represents competition; the green plus sign represents invasiveness; and the orange outward arrow represents over-fishing.

$x(t)$	population of prey
$y(t)$	population of one predator
$z(t)$	population of another (invasive) predator
a	growth rate parameter of x
b	preying effect of y on x
c	preying effect of z on x
d	death rate parameter of the predator y in the absence of prey x
e	growth rate parameter of z
h_1	harvesting effect on x
h_2	harvesting effect on z
α	competition effect of z on y
β	competition effect of y on z

Table 1: The functions and parameters in model (A). All parameters are positive.

We call this model (A) and explain the notation in Table 1.

B. To simplify computations and analysis of model (A), we will proceed by analyzing simpler models and then building the results up. First, we will consider the case when there is *no harvesting* and there is equal competition between the predators, that is, $h_1 = 0 = h_2$

and $\alpha = \beta$; call this model (B):

$$\begin{cases} x' &= ax - bxy - cxz \\ y' &= -dy + bxy - \alpha yz \\ z' &= ez + cxz - \alpha yz. \end{cases} \quad (\text{B})$$

Investigations of this model can be found in Sections 2.1, 2.2, and 3.

C. Then, in Section 4, we consider the effects of harvesting. Section 4.1 covers the case when only the menhaden is harvested and there is equal competition between the predators, that is, $h_1 \neq 0$ and $\alpha = \beta$; call this model (C):

$$\begin{cases} x' &= ax - bxy - cxz - h_1x \\ y' &= -dy + bxy - \alpha yz \\ z' &= ez + cxz - \alpha yz. \end{cases} \quad (\text{C})$$

D. Section 4.2 covers the case when only the catfish is harvested and there is equal competition between the predators, that is, $h_2 \neq 0$ and $\alpha = \beta$; call this model (D):

$$\begin{cases} x' &= ax - bxy - cxz \\ y' &= -dy + bxy - \alpha yz \\ z' &= ez + cxz - \alpha yz - h_2z. \end{cases} \quad (\text{D})$$

E. Next, Section 5 considers the case when there is unequal competition between the predators. Sections 5.1 and 5.2 cover the case when there is no harvesting, that is, $h_1 = 0 = h_2$ and $\alpha \neq \beta$; call this model (E):

$$\begin{cases} x' &= ax - bxy - cxz \\ y' &= -dy + bxy - \alpha yz \\ z' &= ez + cxz - \beta yz. \end{cases} \quad (\text{E})$$

F. Finally, Section 5.3 considers the case when the prey is not harvested but one of the predators is harvested and there is unequal competition between the predators, that is, $h_1 = 0 \neq h_2$ and $\alpha \neq \beta$; call this model (F):

$$\begin{cases} x' &= ax - bxy - cxz \\ y' &= -dy + bxy - \alpha yz \\ z' &= ez + cxz - \beta yz - h_2z. \end{cases} \quad (\text{F})$$

Student Exploration 1: Understanding the models and parameters.

1. The predator effect rates of y and z on the prey x are given by $\pm bxy$ and $\pm cxz$, respectively. How should the system be modified to consider the reality that the effect of the presence of either predators on x may not be the same as the effect of the absence of prey on the predators?
2. If one predator is a stronger competitor than the other predator, what is the corresponding relationship between α and β ?

3. In any of the models, z is an invasive species that will not die in the absence of x . What does it mean when ez replaced by $-ez$, where $e > 0$?
4. If one assumes logistic growth for either the prey or one of the predators, how is the system modified?
5. How does one consider various harvesting scenarios, such as constant, periodic, and delayed harvesting?

2.1 Invariant planes

Since populations are non-negative, we will restrict the domain for x , y and z to the non-negative octant $\{(x, y, z) | x \geq 0, y \geq 0, z \geq 0\}$. By definition, a surface is invariant with respect to a system of differential equations if every solution that starts on the surface does not escape the surface. In our case we will show that coordinate planes are invariant with respect to the system (B). The biological interpretation of invariant planes is that if a species is extinct, then it will not reappear. To prove that a surface is invariant we will use the following theorem from [1].

Theorem 2.1. *Let S be a smooth closed surface without boundary in $\mathbb{R}^3$ and*

$$\begin{cases} x' &= f_1(x, y, z) \\ y' &= f_2(x, y, z) \\ z' &= f_3(x, y, z) \end{cases} \quad (2.1)$$

where f , g , and h are continuously differentiable functions. Suppose that $\mathbf{n}$ is a normal vector to the surface S at (x, y, z) , and for all $(x, y, z) \in S$ we have that

$$\mathbf{n} \cdot (x', y', z') = 0.$$

Then S is invariant with respect to the system (2.1).

Consider the system (B) and the problem of finding its invariant planes. Let S be the plane $z = 0$, then the vector $\mathbf{n} = (0, 0, 1)$ is always normal to S , and at any point $(x, y, 0) \in S$ the following is true:

$$(x', y', z') \cdot \mathbf{n} = (ax - bxy, -dy + bxy, 0) \cdot (0, 0, 1) = 0$$

and consequently, by the above theorem, the plane $z = 0$ is invariant with respect to the system (B).

Student Exploration 2: Computing invariant planes.

1. Show that the planes $x = 0$ and $y = 0$ are invariant with respect to the system (B).
2. Analyze the invariant planes of systems (A) to (F).
3. Show that, if there is no competition between y and z , the plane defined by $S = \{(x, y, z) : ax - dy + ez = 0\}$ is an invariant plane.

2.2 Reduced planar systems

A standard method of analyzing our three-species model is by considering the resulting two-species models; in particular, what happens to the system (B) when $z = 0$, $y = 0$, or $x = 0$?

No catfish

Next, we will look into each of the three reduced planar systems. Assume that there is only one predator by setting $z = 0$. Then the system (B) reduces to the classic Lotka-Volterra prey-predator system.

$$\begin{cases} x' &= x(a - by) \\ y' &= y(-d + bx) \\ z' &= 0. \end{cases} \quad (2.2)$$

This system is well-studied. It has two equilibria, namely, $(0, 0, 0)$ and $(d/b, a/b, 0)$, and it can be shown that system (2.2) has closed trajectories centered at $(d/b, a/b, 0)$. For details on this analysis, the reader is referred to [5].

No striped bass

In the case $y = 0$, or when a trajectory starts on the plane $y = 0$, the system (B) reduces to the following equations:

$$\begin{cases} x' &= x(a - cz) \\ y' &= 0 \\ z' &= z(e + cx). \end{cases}$$

From equation $z' = z(e + cx) > 0$, as the derivative is always positive, it follows that $z(t) \rightarrow \infty$ as $t \rightarrow \infty$, which is consistent with the fact that z is the invader. Expressing $\frac{dz}{dx} = z'/x'$ gives the following separable differential equation

$$\frac{dz}{dx} = \frac{z(e + cx)}{x(a - cz)}$$

which can be solved in the $x - z$ plane implicitly

$$\int \left(\frac{a}{z} - c \right) dz = \int \left(\frac{e}{x} + c \right) dx$$

$$a \ln z - cz + K = e \ln x + cx, \quad (2.3)$$

where K is a constant. Figure 3 illustrates the trajectories' behavior in the x - z -plane for some particular values of the parameters. The graph shows that as time $t \rightarrow \infty$, the invader $z \rightarrow \infty$ while the prey gets depleted $x \rightarrow 0$.

Figure 3: A family of trajectories in the x - z -plane of the implicit solution (2.3) with coefficients $a = c = e = 1$.

Student Exploration 3. Analyzing resulting two-species systems.
Consider system (B).

1. Biologically, what does it mean when $x = 0$? when $y = 0$? $z = 0$?
2. Express the reduced system when $x = 0$ and solve the resulting separable equation for $\frac{dy}{dz}$. Create a graph that illustrates the trajectories in y - z -plane

3 Three-species model without harvesting

Here, we will consider the system given by (B), which we write again here:

$$\begin{cases} x' &= ax - bxy - cxz \\ y' &= -dy + bxy - \alpha yz \\ z' &= ez + cxz - \alpha yz \end{cases} \quad (B)$$

3.1 Equilibria for (B)

Let us compute the set of equilibrium points (x, y, z) of the system (B). These points, also called fixed points, stationary solutions, or zeroes, are solutions that do not change with time, that is, $x' = y' = z' = 0$. We have:

$$\begin{cases} x = 0 & \text{or} & a - by - cz = 0 \\ y = 0 & \text{or} & bx - d - \alpha z = 0 \\ z = 0 & \text{or} & e + cx - \alpha y = 0 \end{cases}$$

Observe that computing equilibrium points requires solving equations, a general theme in mathematics. Besides the equilibrium $E_0 = (0, 0, 0)$, we obtain four more equilibria:

$$E_1 = \left(0, \frac{e}{\alpha}, \frac{-d}{\alpha}\right), E_2 = \left(\frac{-e}{c}, 0, \frac{a}{c}\right), E_3 = \left(\frac{d}{b}, \frac{a}{b}, 0\right),$$

$$E_4 = \left(\frac{cd - be + \alpha a}{2bc}, \frac{cd + be + \alpha a}{2\alpha b}, \frac{\alpha a - (cd + be)}{2\alpha c}\right).$$

the last of which arises from solving the system of linear equations

$$\begin{cases} a - by - cz = 0 \\ bx - d - \alpha z = 0 \\ e + cx - \alpha y = 0 \end{cases}$$

Let us call E_0, E_1, E_2, E_3 our boundary equilibrium points because at least one of the three components is equal to 0. We observe that equilibria E_1 and E_2 are not biologically relevant because each contains a negative component. Hence, we will only look at E_0, E_3 , and E_4 more closely.

Now, we want the components of E_4 to be all positive. Observe that the y -component is always positive. For the x -component to be positive, we require

$$cd - be + \alpha a > 0 \quad \text{or} \quad \frac{be - cd}{a} < \alpha. \quad (3.1)$$

For the z -component to be positive, we require

$$\alpha a - (cd + be) > 0 \quad \text{or} \quad \frac{cd + be}{a} < \alpha. \quad (3.2)$$

Since it is true that $(be - cd)/a < (be + cd)/a$ for all positive parameters b, c, d, e , it follows that by choosing $\alpha > \alpha_{\text{crit}}$, where

$$\alpha_{\text{crit}} = \frac{cd + be}{a},$$

all components of E_4 are positive. Let us summarize our results into a theorem:

Theorem 3.1. *Suppose $\alpha > \alpha_{\text{crit}} = (cd + be)/a$. Then the system (B) has three biologically relevant equilibria, namely, $E_0 = (0, 0, 0)$, $E_3 = (d/b, a/b, 0)$, and*

$$E_4 = \left(\frac{cd - be + \alpha a}{2bc}, \frac{cd + be + \alpha a}{2\alpha b}, \frac{\alpha a - (cd + be)}{2\alpha c}\right).$$

Biologically, this means that there exists a possibility when all three species co-exist if both predators have equal competition effects on each other and when this competition parameter α is greater than α_{crit} . Also observe also that when $\alpha = \alpha_{\text{crit}}$, this equilibrium E_4 reduces to equilibrium E_3 . In this case, we say that α_{crit} is a bifurcation value. Some students may be ready to proceed with a deeper study of bifurcation analysis, a good reference for this topic is [3].

In the next section, we will analyze the stability of these three equilibria using linear stability analysis.

3.2 Elementary dynamical systems theory

We will first state some basic definitions and results from dynamical systems which will be then used to analyze the stability of the three equilibria of (B).

Definition 3.2. An equilibrium point $\bar{w} = (\bar{x}, \bar{y}, \bar{z})$ is called **stable** if a solution $w(t) = (x(t), y(t), z(t))$ based nearby remains close to $\bar{w}$ for all time. Otherwise, the point $\bar{w}$ is called an unstable equilibrium point. An equilibrium point is (locally) **asymptotically stable** if it is stable and the state of the system converges to the equilibrium point as time increases.

These definitions of the stability of equilibria may be used as a good discussion point about the use of real analysis in dynamical systems. It may be a good exercise to ask students to write these definitions in terms of limit statements. The definitions capture the essence of the concept of stability but they do not indicate computational steps to determine the stability of equilibria.

In order to classify the stability of our equilibria, the definition requires that we characterize the behavior of solutions near our equilibria. This is accomplished by linearizing our system (B). Students have been introduced to the concept of linearization from their Differential Calculus courses; they know that the tangent line provides to a nonlinear function at a point in its domain a good approximation of the graph of the function. Analogously, the behavior of nonlinear systems such as (B) near the equilibrium point is similar to the behavior of linear systems near that equilibrium point. This is the so-called Hartman-Grobman Theorem and we refer to [1], [3], [7] for proof and the precise statement.

Towards this end, we consider the linearized system

$$\dot{w}(t) = J(\bar{w})w, \quad (3.3)$$

where $w = (x(t), y(t), z(t))$ and $J(w)$ is the 3-by-3 Jacobian matrix given by

$$J(x, y, z) = \begin{pmatrix} a - by - cz & -bx & -cx \\ by & bx - d - \alpha z & -\alpha y \\ cz & -\alpha z & e + cx - \alpha y \end{pmatrix}. \quad (3.4)$$

Entries of the Jacobian matrix $J = (a_{ij})$ are obtained by taking the partial derivatives,

$$a_{ij} = \frac{\partial f_i}{\partial x_j}, \quad \text{where} \quad (x_1, x_2, x_3) = (x, y, z).$$

For example,

$$a_{11} = \frac{\partial f_1}{\partial x} = a - by - cz, \quad a_{12} = \frac{\partial f_1}{\partial y} = -bx, \quad a_{13} = \frac{\partial f_1}{\partial z} = -cx.$$

When $J(\bar{w})$ has no eigenvalues with zero real part, then $\bar{w}$ is called a **hyperbolic equilibrium point** and the asymptotic behavior of solutions near $\bar{w}$ is determined by the linearization (3.3). If any one of the eigenvalues of $J(\bar{w})$ has a zero real part, then interesting behaviors may occur. Linear stability analysis is accomplished via a fundamental theorem [1], [3], [7]:

Theorem 3.3. *An equilibrium point $\bar{w}$ is asymptotically stable if all the eigenvalues of $J(\bar{w})$ have negative real parts. If at least one of the eigenvalues of $J(\bar{w})$ has a positive real part, then the equilibrium point is unstable.*

Suppose that the three eigenvalues of $J(\bar{w})$ are $\lambda_1 < 0$, $\lambda_2 = 0$, and $\lambda_3 > 0$ with corresponding eigenvector v_1, v_2, v_3 . Solutions which start close to the equilibrium point $\bar{w}$ will decay in the direction of v_1 and will grow in the direction of v_3 . Since $\lambda_2 = 0$, we cannot conclude from linearization whether the solutions decay or grow in the direction of v_2 . The spaces spanned by the eigenvectors v_1, v_3 are called the local stable and local unstable manifolds of $\bar{w}$, respectively; the space spanned by the eigenvector v_2 is called the local center manifold of $\bar{w}$. At this point, a manifold may be briefly described as a generalization of a linear subspace of $\mathbb{R}^n$. Points, lines, planes, arcs, and spheres are examples of manifolds. Students who become interested in this topic may want to look into the area of mathematics called Differential Geometry.

To make a direct conclusion about the stability of an equilibrium, one has to analyze the nature of the eigenvalues, that is, the roots of the characteristic equation $\det(J(\bar{w}) - \lambda I) = 0$. In some cases, finding the roots of the characteristic equation may be obtained by hand. Indeed, for the system that we are considering in this project, the characteristic equation is a third-degree polynomial with real coefficients. In case solving the roots is not possible, then there are some analytic, algebraic, and computational options. In this paper, we will demonstrate these options.

The following theorem summarizes the existence of stable, center, and unstable manifolds for a three-dimensional system and is oftentimes referred to as the Center Manifold Theorem. For the precise statement and proof, we refer to [1], [3], [7].

Theorem 3.4. *Suppose f is a smooth vector field in $\mathbb{R}^3$. Assume that the system $\dot{w} = f(w)$ has an equilibrium point $\bar{w}$ and its linearization at $\bar{w}$ is given by $\dot{w} = J(\bar{w})w$. Suppose $\sigma_s, \sigma_c, \sigma_u$, contain the negative, zero, and positive eigenvalues of $J(\bar{w})$, respectively. Let E^s, E^c, E^u be the eigenspaces associated with $\sigma_s, \sigma_c, \sigma_u$, respectively. Then there exist smooth stable W^s , center W^c , and unstable W^u manifolds tangent to E^s, E^c , and E^u , respectively at $\bar{w}$. The stable and unstable manifolds are unique, but W^c need not be.*

3.3 Stability for (B)

We have seen that there are three biologically relevant equilibrium points. Let us call E_0 the trivial equilibrium point, E_3 the catfish-free boundary equilibrium point, and E_4

the interior co-existence equilibrium point. In this section, we will show that they are all unstable.

Stability Analysis for E_0

The equilibrium point E_0 is unstable. To see this, observe that the matrix $J(E_0) = J(0, 0, 0)$ is given by

$$J(0, 0, 0) = \begin{pmatrix} a & 0 & 0 \\ 0 & -d & 0 \\ 0 & 0 & e \end{pmatrix}$$

with eigenvalues $a > 0, -d < 0, e > 0$, with corresponding eigenvectors $(1, 0, 0)$, $(0, 1, 0)$, and $(0, 0, 1)$. According to Theorem 3.3, E_0 is an unstable equilibrium. By Theorem 3.4, we know that the negative eigenvalue has a corresponding one-dimensional stable manifold, or curve, tangent to the eigenvector $(0, 1, 0)$ at the equilibrium $(0, 0, 0)$. This stable curve is actually the y -axis which means that $y(t) \rightarrow 0$ as $t \rightarrow \infty$; this is biologically relevant as in the absence of x , the prey, the predator y will become extinct. Corresponding to the two positive eigenvalues, there is a two-dimensional unstable manifold or a plane, tangent at the equilibrium $(0, 0, 0)$ and spanned by the vectors $(1, 0, 0)$ and $(0, 0, 1)$. This two-dimensional unstable manifold is the xz -plane which from a biological perspective means that both the prey and the invader will grow without a boundary in the absence of y , i.e. $x(t) \rightarrow \infty$ and $z(t) \rightarrow \infty$.

Since $J(E_0)$ has two positive eigenvalues and one negative eigenvalue, E_0 is a hyperbolic equilibrium point. Moreover, in this case, we say that E_0 is a hyperbolic saddle point.

Stability Analysis for E_3

The equilibrium $E_3 = \left(\frac{d}{b}, \frac{a}{b}, 0\right)$ is an unstable non-hyperbolic equilibrium point. To see this, the Jacobian at E_3 is given by the following matrix

$$J\left(\frac{d}{b}, \frac{a}{b}, 0\right) = \begin{pmatrix} 0 & -d & -cd/b \\ a & 0 & -\alpha a/b \\ 0 & 0 & (cd + be - \alpha a)/b \end{pmatrix},$$

with characteristic equation $g(x) = (x - \lambda_s)(x^2 + ad)$ where $\lambda_s = \frac{cd + be - \alpha a}{b}$. The three eigenvalues are λ_s and the two purely imaginary eigenvalues $\pm i\sqrt{ad}$.

Since we assume that $\alpha > \alpha_{\text{crit}}$, observe that λ_s is negative and hence by Theorem 3.4, there is a one-dimensional stable manifold at E_3 tangent to the eigenvector spanned by

$$(\beta_1\beta_3 - \beta_2d, a\beta_1 + \beta_2\beta_3, \beta_3^2 + ad),$$

where $\beta_1 = -cd/b$, $\beta_2 = -\alpha a/b$, and $\beta_3 = \lambda_s$.

Corresponding to the purely imaginary eigenvalues $\pm i\sqrt{ad}$, there exists a two-dimensional center manifold at E_3 tangent to the space spanned by the eigenvectors

$$\begin{pmatrix} 0 \\ 1 \\ 0 \end{pmatrix} \pm \begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix} \sqrt{\frac{d}{a}} i.$$

The eigenspace spanned by these vectors is the xy -plane. As not all eigenvalues have negative real parts, this equilibrium is unstable.

Stability Analysis for E_4

Next, we will examine the stability of the equilibrium $E_4 = (x^*, y^*, z^*)$, where

$$x^* = \frac{cd - be + \alpha a}{2bc}, y^* = \frac{cd + be + \alpha a}{2ab}, z^* = \frac{\alpha a - (cd + be)}{2\alpha c}.$$

Recall that we assume that $\alpha > \alpha_{\text{crit}}$ so that x^*, y^*, z^* are always positive. The Jacobian matrix (3.4) at this point is given by

$$J(x^*, y^*, z^*) = \begin{pmatrix} 0 & -bx^* & -cx^* \\ by^* & 0 & -\alpha y^* \\ cz^* & -\alpha z^* & 0 \end{pmatrix}.$$

where (x^*, y^*, z^*) is the solution to the system

$$\begin{cases} a - by - cz = 0 \\ bx - d - \alpha z = 0 \\ cx + e - \alpha y = 0. \end{cases}$$

To find the eigenvalues λ , we need to analyze the roots of the characteristic equation

$$-\lambda^3 - (b^2x^*y^* + c^2x^*z^* - \alpha^2y^*z^*)\lambda + 2bc\alpha x^*y^*z^* = 0,$$

that is,

$$\lambda^3 + B\lambda + C = 0, \tag{3.5}$$

where $B = b^2x^*y^* + c^2x^*z^* - \alpha^2y^*z^*$ and $C = -2bc\alpha x^*y^*z^*$. Solving for the closed-form of the roots of (3.5) is not a straightforward computation.

Since we are not able to compute the exact roots of the characteristic equation, let us present an analytic method of analyzing the roots using the Intermediate Value Theorem from Calculus I. Consider $g(x) = x^3 + Bx + C$. Since $y = g(x)$ has a positive leading coefficient for x^3 , it follows that the graph of $y = g(x)$ is ultimately increasing, positive, and unbounded. This implies that there exists $\gamma > 0$ such that $g(\gamma) > 0$. However, we also observe that $g(0) = C < 0$. Thus, it follows from the Intermediate Value Theorem that there exists $0 < \beta < \gamma$ such that $g(\beta) = 0$. The existence of this positive real root for $y = g(x)$ tells us that one of the eigenvalues is a positive real number. Hence, the equilibrium E_4 is unstable!

Summarizing our results on the behavior of the equilibria of the system (B), we have

Theorem 3.5. Suppose $\alpha > \alpha_{\text{crit}} = (cd + be)/a$. Then, system (B) has two boundary equilibrium points and one interior equilibrium point. They are all unstable:

$$E_0 = (0, 0, 0), E_3 = \left(\frac{d}{b}, \frac{a}{b}, 0\right), E_4 = \left(\frac{cd - be + \alpha a}{2bc}, \frac{cd + be + \alpha a}{2\alpha b}, \frac{\alpha a - (cd + be)}{2\alpha c}\right).$$

Student Exploration 4. Using algebra and calculus to analyze characteristic equations. Consider the cubic polynomial $g(x) = x^3 + Bx + C$ where $C < 0$. Recall from the Fundamental Theorem of Algebra that g will have at most three roots; furthermore, g can either have three real roots or one real root and a pair of complex conjugate roots.

1. Draw possible pictures of $y = g(x)$ where g has three real roots.
2. Draw possible pictures of $y = g(x)$ where g has one real root and a pair of complex roots.

3.4 Phase portrait near co-existence equilibrium for (B)

We can also use computer power to analyze the roots of equation (3.5). Using MATLAB, we can calculate the eigenvalues and the eigenvectors, we can create a time-evolution of the functions, and we can also create a phase portrait. Consider the following particular values of the parameters:

a	growth rate parameter of x	0.5
b	preying effect of y on x	0.01
c	preying effect of z on x	0.01
d	death rate parameter of the predator y in the absence of prey x	0.5
e	growth rate parameter of z	0.5

Table 2: The parameter values used in the simulation are summarized in this table.

Furthermore, we assume in this section that $\alpha = \beta = 0.1$. With these parameter values, the interior coexistence equilibrium point is $E_4 = (275, 30, 20)$ with eigenvalues -1.6046 , -0.8398 , and 2.4444 . The bifurcation value is $\alpha_{\text{crit}} = (cd + be)/a = 0.02$.

Figure 4 shows the phase portrait consisting of trajectories near the interior co-existence equilibrium point E_4 , which is represented in the plot as a red dot. Starting from initial conditions close to the equilibrium E_4 , the phase portrait shows that the trajectories approach what appears to be orbit trajectories on the xy -plane around the boundary equilibrium point E_3 , represented by a yellow dot. This illustrates that the co-existence equilibrium is highly unstable. Equilibrium is possible for some critical positive populations of the three species, and while each species maintains that population level, they may co-exist. If at any instant the population levels are not at the critical sizes, then the effects of competition will drive some of the species to extinction.

4 Three-species model with harvesting

4.1 Overfishing of menhaden

Now, we modify the model (B) to include harvesting of the prey (Atlantic menhaden) $x(t)$. Here, we assume that harvesting of the menhaden occurs at a linear rate, h_1x , for some positive constant h_1 , that is, the harvesting of x happens in direct proportion with its growth:

$$\begin{cases} x' &= ax - bxy - cxz - h_1x \\ y' &= bxy - dy - \alpha yz \\ z' &= ez + cxz - \alpha yz. \end{cases} \quad (\text{C})$$

When harvesting of the prey is accomplished at a higher rate than the prey's growth, we say that overfishing occurs. Defining $A = a - h_1$, we see that overfishing happens when $A < 0$. In case $A > 0$, we observe that we recover system (B) with a replaced by A .

Equilibria for (C)

As before, setting the derivatives equal to zero in (C) solves the equilibrium points. We obtain

$$E_0 = (0, 0, 0), \quad E_1 = \left(0, \frac{e}{\alpha}, \frac{-d}{\alpha}\right), \quad E_2 = \left(\frac{-e}{c}, 0, \frac{a - h_1}{c}\right), \quad E_3 = \left(\frac{d}{b}, \frac{a - h_1}{b}, 0\right),$$

Figure 4: Trajectories behavior for model (B) near equilibrium point $E_4 = (275, 30, 25)$ with initial conditions $(300, 30, 15)$ in blue, $(310, 35, 20)$ in black, and $(320, 30, 20)$ in red. The red dot is the equilibrium E_4 , the yellow dot is $E_3 = (50, 50, 0)$, and the green dot is $E_0 = (0, 0, 0)$. See Table 2 for parameter values.

and, as in the previous model, a fourth equilibrium

$$E_4 = \left(\frac{cd - be + \alpha(a - h_1)}{2bc}, \frac{cd + be + \alpha(a - h_1)}{2ab}, \frac{\alpha(a - h_1) - (cd + be)}{2\alpha c} \right).$$

Let us observe that E_1 , E_2 , and E_3 and E_4 are not biologically relevant as some of their components are negative due to the assumption $a - h_1 < 0$. In particular, when overfishing of menhaden happens, the interior co-existence equilibrium point does not exist.

Theorem 4.1. *Suppose $h_1 > a$. Then the system (C) has only one biologically relevant equilibrium point, $E_0 = (0, 0, 0)$.*

Linearization and stability analysis for (C)

The linearization of (C) is represented by the matrix

$$J(x, y, z) = \begin{pmatrix} a - by - cz - h_1 & -bx & -cx \\ by & bx - d - \alpha z & -\alpha y \\ cz & -\alpha z & cx + e - \alpha y \end{pmatrix}.$$

Let us now analyze the behavior of the system at the only biologically relevant equilibrium point, E_0 . Observe that

$$J(0, 0, 0) = \begin{pmatrix} a - h_1 & 0 & 0 \\ 0 & -d & 0 \\ 0 & 0 & e \end{pmatrix}$$

with eigenvalues $a - h_1 < 0$, $-d < 0$, $e > 0$ and the corresponding eigenvectors are $(1, 0, 0)$, $(0, 1, 0)$, and $(0, 0, 1)$. Since we assume that $h_1 > a$, we have two negative eigenvalues and one positive eigenvalue. Thus, E_0 is unstable. Moreover, using Theorem 3.4, there is an invariant two-dimensional stable manifold that is tangent to the space spanned by eigenvectors $(1, 0, 0)$ and $(0, 1, 0)$, which is the xy -plane. On the xy -plane, solutions approach the equilibrium $E_0 = (0, 0, 0)$, meaning that $x(t) \rightarrow 0$ as $t \rightarrow \infty$ and $y(t) \rightarrow 0$ as $t \rightarrow \infty$. This is biologically relevant as if the prey is overfished, then in time both the prey and the predator will become extinct. In addition, there is also an one-dimensional unstable manifold spanned by the eigenvector $(0, 0, 1)$, or the z -axis, on which $z(t) \rightarrow \infty$ or the catfish will grow without limit.

Student Exploration 5. What happens when the harvesting rate is equal to the growth rate? Analyze the system (C) when $h_1 = a$.

1. Show that there are only two biologically relevant equilibria, $(0, 0, 0)$ and $(d/b, 0, 0)$.
2. Show that both equilibria are unstable.
3. Sketch a phase portrait.

4.2 Harvesting of catfish

In this section, we ask, will harvesting of the catfish solve its invasive effect on the Chesapeake Bay? In other words, does it help to *eat the invaders* [2]?

Let us modify the model (B) to include harvesting of one of the predators, the catfish. Assume that harvesting of the catfish occurs at a linear rate $h_2 z$, for some positive constant h_2 , that is, the harvesting of z happens in direct proportion to its growth. We get

$$\begin{cases} x' &= ax - bxy - cxz \\ y' &= -dy + bxy - \alpha yz \\ z' &= ez + cxz - \alpha yz - h_2 z, \end{cases} \quad (\text{D})$$

which is equivalent to

$$\begin{cases} x' &= ax - bxy - cxz \\ y' &= -dy + bxy - \alpha yz \\ z' &= Ez + cxz - \alpha yz \end{cases} \quad (4.1)$$

where $E = e - h_2$. Note that unlike the other parameters, E may be positive, negative, or zero.

Equilibrium points for (D)

We set the derivatives equal to zero and find four boundary equilibrium points

$$E_0 = (0, 0, 0), E_1 = \left(0, \frac{E}{\alpha}, \frac{-d}{\alpha}\right), E_2 = \left(\frac{-E}{c}, 0, \frac{a}{c}\right), E_3 = \left(\frac{d}{b}, \frac{a}{b}, 0\right),$$

and one interior co-existence equilibrium point

$$E_4 = \left(\frac{cd - bE + \alpha a}{2bc}, \frac{cd + bE + \alpha a}{2\alpha b}, \frac{\alpha a - (cd + bE)}{2\alpha c}\right).$$

For the equilibrium E_4 to exist, we need to require that its components are positive:

$$\begin{cases} cd - bE + \alpha a &> 0 \\ cd + bE + \alpha a &> 0 \\ \alpha a - (cd + bE) &> 0. \end{cases}$$

Now, let us study parameter intervals using these inequalities. Manipulation of the inequalities depends on the parameter that one wishes to investigate. As previously, let us find the bounds for the competition parameter α . Toward this end, we have

$$\begin{cases} \alpha a &> bE - cd \\ -\alpha a &< bE + cd \\ \alpha a &> bE + cd. \end{cases}$$

Or, upon combining these inequalities, we have

$$\left| \frac{bE + cd}{a} \right| < \alpha. \quad (4.2)$$

The equilibrium point E_4 exists when the competition parameter α satisfies this inequality.

Next, let us analyze model **D** with respect to the sign $E = e - h_2$, where e is the growth rate and h_2 is the harvesting parameter of the catfish.

Case 1. $E < 0$. This is the case when $e < h_2$. We shall call this the overfishing of the catfish population, when the rate of harvesting exceeds the growth rate of the species z . From the analysis above, the equilibrium E_4 is biologically relevant as long as the competition parameter is sufficiently large. If the parameter α is not big enough, then the equilibrium E_4 will not have positive components and hence E_4 will not be biologically relevant. This means that even when there is overfishing of the catfish, all three species may still co-exist. If the competition strength between the striped bass and the catfish is below the critical value $|bE + cd|/a$, then the three species will not co-exist. Hence, when $E < 0$, there are three boundary equilibrium points, E_0, E_2, E_3 and one interior co-existence equilibrium point E_4 .

Case 2. $E > 0$. We shall call this case (a plain) harvesting. Then the equilibrium E_4 exists as it will have positive components as long as the competition is at a sufficiently large value. This means that even if there is harvesting of catfish, all three species may co-exist. When $E > 0$, there are three equilibrium points E_0, E_3 , and E_4 .

Case 3. $E = 0$. In this case the harvesting rate is exactly equal to the growth rate. Then the equilibrium E_4 exists, that is, it will have positive components provided $-cd + \alpha a > 0$. As a bonus, we can see here that with respect to the competition parameter α , a bifurcation value is $\alpha = cd/a$. When $E = 0$, the equilibrium points are E_0, E_2, E_3 , and E_4 .

These results on the equilibria are summarized in the following theorem.

Theorem 4.2. Suppose $\left| \frac{bE + cd}{a} \right| < \alpha$, where $E = e - h_2$. Then (4.1) has 5 equilibrium points:

$$E_0 = (0, 0, 0), \quad E_1 = \left(0, \frac{E}{\alpha}, \frac{-d}{\alpha}\right), \quad E_2 = \left(\frac{-E}{c}, 0, \frac{a}{c}\right), \quad E_3 = \left(\frac{d}{b}, \frac{a}{b}, 0\right),$$

$$E_4 = \left(\frac{cd - bE + \alpha a}{2bc}, \frac{cd + bE + \alpha a}{2\alpha b}, \frac{\alpha a - (cd + bE)}{2\alpha c}\right).$$

If $E \leq 0$ then E_0, E_2, E_3, E_4 are biologically relevant. If $E > 0$ then E_0, E_3, E_4 are biologically relevant. In particular, the interior co-existence equilibrium point E_4 always exists for any value of E , provided the competition parameter α is large enough.

This theorem highlights the interesting result that when harvesting on the invasive species happens, competition between the two predators must be high enough in order for the three species to co-exist. Competition, in this case, is essential and beneficial to the ecological dynamics of this system.

Linearization and stability analysis for (D)

The linearization is given by the 3-by-3 matrix $\dot{w}(t) = J(\bar{w})w$ where $w = (x(t), y(t), z(t))$ and $J(w)$ is the 3-by-3 Jacobian matrix given by

$$J(x, y, z) = \begin{pmatrix} a - by - cz & -bx & -cx \\ by & bx - d - \alpha z & -\alpha y \\ cz & -\alpha z & E + cx - \alpha y \end{pmatrix}.$$

Equilibrium Point	Characteristic Equation	Eigenvalues	Stability Result						
$E_0(0, 0, 0)$	$(\lambda - a)(\lambda + d)(\lambda - E) = 0$	$a, -d, E$	This equilibrium point exists and is unstable for all values of E .						
$E_2\left(\frac{-E}{c}, 0, \frac{a}{c}\right)$	$(\lambda + \lambda_{t+})(\lambda^2 - aE) = 0,$ $\lambda_{t+} = \frac{bE + cd + \alpha a}{c}$	$-\lambda_{t+}, \pm\sqrt{aE}$	<table><tr><td>$E > 0$</td><td>not an equilibrium</td></tr><tr><td>$E = 0$</td><td>unstable</td></tr><tr><td>$E < 0$</td><td>unstable</td></tr></table>	$E > 0$	not an equilibrium	$E = 0$	unstable	$E < 0$	unstable
$E > 0$	not an equilibrium								
$E = 0$	unstable								
$E < 0$	unstable								
$E_3\left(\frac{d}{b}, \frac{a}{b}, 0\right)$	$(\lambda - \lambda_{t-})(\lambda^2 + ad) = 0,$ $\lambda_{t-} = \frac{bE + cd - \alpha a}{c}$	$\lambda_{t-}, \pm i\sqrt{ad}$	This equilibrium point exists and is unstable for all values of E .						
$E_4(x^*, y^*, z^*)$ $x^* = \frac{cd - bE + \alpha a}{2bc},$ $y^* = \frac{cd + bE + \alpha a}{2\alpha b},$ $z^* = \frac{\alpha a - (cd + bE)}{2\alpha c}$	$\lambda^3 + B\lambda + C = 0,$ $B = b^2x^*y^* + c^2x^*z^* - \alpha^2y^*z^*,$ $C = -2bc\alpha x^*y^*z^*$	The closed-form of roots is not straightforward to compute.	This equilibrium point exists and is unstable for all values of E .						

Table 3: The table presents a summary of the equilibria of model (D) and their stability when harvesting of the catfish happens, where $E = e - h_2$.

As described and demonstrated in the previous section, stability analysis requires analyzing the roots of the resulting characteristic equation for $J(\bar{w})$ where $\bar{w} \in \{E_0, E_2, E_3, E_4\}$. Here, we assume that the competition parameter α satisfies $\alpha > |bE + cd|/a$. A summary of the equilibria and their stability result is presented in Table 3, with $E = e - h_2$, as stated in Theorem 4.2.

As a result, we can say that the policy that recommends eating the catfish to control its invasive growth [2] may not be able to accomplish the following: drive the catfish to extinction, eradicate competition with the striped bass, or affect the menhaden's population growth adversely; however, mathematical analysis shows that overfishing the catfish will still allow all three species to coexist.

5 Mathematical model when $\alpha \neq \beta$

In this section, we investigate the system (A) when the interference between the two predators are not equal, $\alpha \neq \beta$:

$$\begin{cases} x' &= ax - bxy - cxz \\ y' &= -dy + bxy - \alpha yz \\ z' &= ez + cxz - \beta yz. \end{cases} \quad (\text{E})$$

The interference measures the competition effect of one predator over another: when the catfish is more aggressive than the striped bass then $\alpha > \beta > 0$ and when the striped bass is more aggressive than the catfish then $0 < \alpha < \beta$. Observe that if β were negative, then the term $-\beta yz$ in the third equation would mean that the species z acts as a predator on the species y and in this case, the system would model the food chain scenario: z preys on y which preys on x , which is a completely different system than what we are studying. Indeed, a slight modification in the terms of a system of differential equations, such as a change in the sign of the parameters, may pertain to a different biological phenomenon!

5.1 Equilibria for (E)

Setting the derivatives equal to zero yields four boundary equilibrium points and one interior equilibrium point for (E):

$$Q_0 = (0, 0, 0), Q_1 = \left(0, \frac{e}{\alpha}, \frac{-d}{\alpha}\right), Q_2 = \left(\frac{-e}{c}, 0, \frac{a}{c}\right), Q_3 = \left(\frac{d}{b}, \frac{a}{b}, 0\right), \quad (5.1)$$

and

$$Q_4 = \left(\frac{(cd + \alpha a)\beta - \alpha be}{(\alpha + \beta)bc}, \frac{cd + be + \alpha a}{(\alpha + \beta)b}, \frac{a\beta - (cd + be)}{(\alpha + \beta)c}\right). \quad (5.2)$$

Note that Q_1 and Q_2 have negative components and are not biologically possible. Q_0 is the trivial equilibrium and $Q_3 = E_3$ is the equilibrium in the case when $\alpha = \beta$. For the equilibrium point Q_4 to be biologically relevant, all of its components must be positive. Observe that its y -component is always positive while its z -component is positive provided

$$a\beta > cd + be \quad \text{or} \quad \beta > \frac{cd + be}{a}.$$

Observe that the right hand side of the above inequality is the critical value $\alpha_{\text{crit}} = \frac{cd + be}{a}$ obtained in Section 3.1. If $\beta > \alpha_{\text{crit}}$ the z -component of Q_4 will be positive. Let us prove that the condition $\beta > \alpha_{\text{crit}}$ is sufficient for the x -component of Q_4 to be also positive. Using the fact that $\beta > \alpha_{\text{crit}}$, substitute β in the numerator of the x -component as follows

$$(cd + \alpha a)\beta > \frac{(cd + \alpha a)(cd + be)}{a}.$$

The right-hand side of this inequality can be simplified to

$$\frac{(cd)^2 + cdbe + aacd + aabe}{a} = \frac{(cd)^2 + cdbe + aacd}{a} + abe > abe.$$

Thus, $(cd + \alpha a)\beta > abe$, so the first component of Q_4 is positive. If β is larger than some critical value α_{crit} , then there exists an interior equilibrium point. Biologically, this means that co-existence of the three species is possible.

5.2 Linearization and stability analysis for (E)

The linearization of the system (E) is similar to the Jacobian (3.4) except for the third row as given by the following matrix:

$$J(x, y, z) = \begin{pmatrix} a - by - cz & -bx & -cx \\ by & bx - d - \alpha z & -\alpha y \\ cz & -\beta z & cx + e - \beta y \end{pmatrix}. \quad (5.3)$$

At the trivial equilibrium Q_0 , the Jacobian matrix has a diagonal form

$$J(0, 0, 0) = \begin{pmatrix} a & 0 & 0 \\ 0 & -d & 0 \\ 0 & 0 & e \end{pmatrix}$$

and has the same eigenvalues and eigenvectors discussed in section 3.2 for the equilibrium E_0 . Consequently, Q_0 is also unstable. Furthermore, observe that the Jacobian $J(Q_3)$ is similar to the Jacobian at the equilibrium E_3 except for one term in the third row:

$$J\left(\frac{d}{b}, \frac{a}{b}, 0\right) = \begin{pmatrix} 0 & -d & -cd/b \\ a & 0 & -\alpha a/b \\ 0 & 0 & (cd + be - \beta a)/b \end{pmatrix},$$

with one real eigenvalue $(cd + be - \beta a)/b$ and the purely imaginary eigenvalues $\pm i\sqrt{ad}$. For $\beta > \alpha_{\text{crit}}$, the real eigenvalue is negative and by the Center Manifold Theorem, there is a one-dimensional stable manifold tangent at $(d/b, a/b, 0)$ to the corresponding eigenvector. Since not all eigenvalues have negative real parts, the equilibrium Q_3 is also unstable.

Finally, let us analyze the stability of Q_4 via its Jacobian $J(Q_4)$. Like before, the computation of the roots of the resulting characteristic equation is not straightforward. Here, let us demonstrate another technique in analyzing the roots of polynomials via an algebraic result called the Routh-Hurwitz Criteria. This theorem gives a necessary and sufficient condition for a polynomial to have only zeros with negative real parts [9]. Here, we include this theorem's version for the particular case of a third-degree polynomial:

Theorem 5.1. (Routh-Hurwitz Criteria) *For a third-degree polynomial of the form $\lambda^3 + A\lambda^2 + B\lambda + C = 0$, the three roots will have negative real parts if and only if the following three conditions are satisfied*

$$A, C > 0 \quad \text{and} \quad AB - C > 0.$$

From this theorem follows that if at least one of the coefficients A or C is not strictly positive, then it is not possible for all three roots to have negative real parts and hence the equilibrium point will be unstable.

Student Exploration 6. Using algebraic results to investigate characteristic equations. Analyze the stability of the interior co-existence equilibrium point Q_4 .

1. Verify that the characteristic equation corresponding to the equilibrium point Q_4 is

$$\lambda^3 + (b^2x^*y^* + c^2x^*z^* - \alpha\beta y^*z^*)\lambda - bc(\alpha + \beta)x^*y^*z^* = 0.$$

2. Use the Routh-Hurwitz Criteria to verify that Q_4 is unstable.

Theorem 5.2. Suppose $\beta > \frac{cd + be}{a}$. Then the system (E) has the following biologically relevant equilibria:

$$Q_0 = (0, 0, 0), Q_3 = \left(\frac{d}{b}, \frac{a}{b}, 0\right), \quad \text{and} \quad Q_4 = \left(\frac{(cd + \alpha a)\beta - \alpha be}{(\alpha + \beta)bc}, \frac{cd + be + \alpha a}{(\alpha + \beta)b}, \frac{a\beta - (cd + be)}{(\alpha + \beta)c}\right).$$

They are all unstable.

5.3 Harvesting of catfish

In this part, let us analyze the model when the competition interference between the striped bass and the catfish is not equal with the additional condition that the catfish is also being harvested at a linear rate h_2z . In fact, we assume here that $\alpha > \beta > \frac{cd + bE}{a}$, that is, between the two competing predators, the catfish causes more harm towards the striped bass' population. Here, $E = e - h_2$. We have,

$$\begin{cases} x' &= ax - bxy - cxz \\ y' &= -dy + bxy - \alpha yz \\ z' &= Ez + cxz - \beta yz. \end{cases} \quad (F)$$

Like before, a bifurcation occurs when $e = h_2$; the results are summarized in Table 4.

6 Numerical simulations

While the previous sections utilized theoretical analysis to investigate the local stability of equilibrium points, here we will use MATLAB to numerically simulate the systems. Numerical simulations and their graphs offer numerical and visual perspectives on the long term behavior of the three fish species.

6.1 Discovery via numerical time-evolutions

Figure 5 shows the long-term behavior of the fish populations for some particular values of the parameters a, b, c, d, e given in Table 2 with initial conditions (100, 10, 10). Panel (a) illustrates the populations when $\alpha = \beta$ and the two predators are equally competitive. The catfish (represented by the blue curve) grows without bound. The other two species die out: the striped bass (represented by the green curve) dies out earlier than the menhaden (represented by the red curve). This behaviour among the three species is still reflected

Equilibrium Point	Characteristic Equation	Eigenvalues	Stability Result						
$E_0(0, 0, 0)$	$(\lambda - a)(\lambda + d)(\lambda - E) = 0$	$a, -d, E$	This equilibrium point exists and is unstable for all values of E .						
$E_2\left(\frac{-E}{c}, 0, \frac{a}{c}\right)$	$(\lambda + \lambda_{t+})(\lambda^2 - aE) = 0,$ $\lambda_{t+} = \frac{bE + cd + \alpha a}{c}$	$-\lambda_{t+}, \pm\sqrt{aE}$	<table><tr><td>$E > 0$</td><td>not an equilibrium</td></tr><tr><td>$E = 0$</td><td>unstable</td></tr><tr><td>$E < 0$</td><td>unstable</td></tr></table>	$E > 0$	not an equilibrium	$E = 0$	unstable	$E < 0$	unstable
$E > 0$	not an equilibrium								
$E = 0$	unstable								
$E < 0$	unstable								
$E_3\left(\frac{d}{b}, \frac{a}{b}, 0\right)$	$(\lambda - \lambda_{t-})(\lambda^2 + ad) = 0,$ $\lambda_{t-} = \frac{bE + cd - \beta a}{c}$	$\lambda_{t-}, \pm i\sqrt{ad}$	This equilibrium point exists and is unstable for all values of E .						
$E_4(x^*, y^*, z^*)$ where $x^* = \frac{(cd + \alpha a)\beta - \alpha bE}{(\alpha + \beta)bc},$ $y^* = \frac{cd + bE + \alpha a}{(\alpha + \beta)b},$ $z^* = \frac{a\beta - (cd + bE)}{(\alpha + \beta)c}$	$\lambda^3 + B\lambda + C = 0$, where $B = b^2x^*y^* + c^2x^*z^* - \alpha\beta y^*z^*,$ $C = -bc(\alpha + \beta)x^*y^*z^*$	The closed-form of roots is not straightforward to compute.	This equilibrium point exists and is unstable for all values of E .						

Table 4: The table presents a summary of the equilibria of model (F) and their stability in the case there is unequal competition interference between predators, $\alpha \neq \beta$, and when harvesting of the catfish happens $E = e - h_2$.

in the case when $\alpha > \beta$, that is, the catfish is a stronger competitor than the striped bass as shown in panel (b). If we assume that the catfish is less competitive or less aggressive than the striped bass $\alpha < \beta$ then as shown in panel (c), the catfish becomes extinct while the menhaden and the striped bass co-exist. Furthermore, in this case, we observe periodic shifted behavior between menhaden and bass that is typically found in two-species predator-prey models.

However, in reality the blue catfish is much more competitive in the following sense. According to [6], about 75% of all fish biomass in the Virginia Coastal waters consists of the blue catfish and the catfish actually also preys on many other fish species, not just the menhaden. Hence, it is biologically more realistic to assume that $\alpha > \beta$. Our model (see Figure 5 (b)) predicts that ultimately, the blue catfish grows in an unbounded manner compared with the native species, the striped bass and the Atlantic menhaden. If no serious measures are taken to prevent the widespread of the invasive blue catfish, the native species will be seriously affected and may even become extinct.

Now, panel (d) in Figure 5 presents a simulation of the time-evolution of the three species' populations when there is harvesting of the catfish with the more realistic case of $\alpha > \beta$. If the harvesting term is assumed to be a linear rate h_2z , and the harvesting parameter h_2 is high enough, then it is possible for the catfish and the menhaden to

Figure 5: Menhaden, striped bass, and catfish distributions over time for the following values of the parameters: $a = d = e = 0.5$, $b = c = 0.01$ with initial conditions $(100, 10, 10)$. Panels (a) $\alpha = \beta = 0.5$, (b) $\alpha = 0.8$ and $\beta = 0.2$, (c) $\alpha = 0.2$ and $\beta = 0.8$, (d) $\alpha = 0.8$, $\beta = 0.2$ and harvesting parameter of the catfish is $h_2 = 1$.

co-exist, and they will exhibit the typical predator-prey phase-shifted periodic behavior. However, the striped bass dies out.

Figure 6: Time-evolutions on the population of menhaden, striped bass, and catfish when there is harvesting of catfish. The following values of the parameters were used: $a = d = e = 0.5$, $b = c = 0.01$, $\alpha = 0.8$, $\beta = 0.2$ with initial conditions $(100, 10, 10)$. Panels (a) $h_2 = 0.4$, (b) $h_2 = 0.5$, (c) $h_2 = 0.8$, (d) $h_2 = 1.5$.

6.2 Further numerical investigations: harvesting of aggressive catfish

Continuing with the more biologically realistic assumption that $\alpha > \beta$, Figure 6 shows the effect of harvesting on the catfish. Here, we would like to investigate if harvesting is able to control the invasive effect of the catfish on the Chesapeake Bay. In these simulations, we will keep $e = 0.5$ constant, where e is the growth parameter for the catfish.

Panel (a) shows that a harvesting rate $h_2 = 0.4$ is not sufficient to control the population growth of the catfish. Panel (b) shows that with a harvesting rate of $h_2 = 0.5 = e$, the (blue) population curve for the catfish exhibits bounded growth. Thus, we say that in this case, harvesting is able to control the growth of the catfish. Unfortunately, the menhaden eventually dies out. The second predator (the striped bass) dies even before the menhaden, due to the decreasing population of its prey and the aggressive behavior of its competitor.

Now, what happens when the harvesting rate of the catfish exceeds its growth rate, that is, when overfishing of the catfish happens? Panels (c) and (d) show two cases, with $h_2 = 0.8$ and $h_2 = 1.5$ respectively.

Panel (c) shows that with aggressive harvesting $h_2 = 0.8 > 0.5 = e$, a periodic phase-shifted behavior becomes evident for the catfish and its menhaden prey. The striped bass, which is a second predator and also a competitor to the catfish, dies out.

Panel (d) shows that with even more aggressive harvesting $h_2 = 1.5 > 0.5 = e$, a periodic phase-shifted behavior also occurs between the predator and prey. The striped bass also dies out in this case. Hence, we can conclude that it is possible to control the exponential growth of the invasive species with aggressive harvesting.

Finally, observe that between panels (c) and (d) in Figure (6), we notice two interesting observations as h_2 increases, that is, when harvesting of catfish becomes more aggressive: (1) the local maximum values of the menhaden exceed the local maximum values of the catfish; and (2) the periods for both menhaden and catfish as they exhibit their phase-shifted predator-prey behavior decrease. These observations may give rise to further inquiries on how aggressive harvesting affects the resulting predator-prey relationship between menhaden and catfish.

6.3 Further numerical investigations: harvesting of the catfish with equally competitive striped bass

Another interesting long-term behavior of the three fish species in this project is visualized in Figure 7. Here, we consider the case when the competition effects are equal on both predators. Also, we assume that there is harvesting of the catfish. The values for h_2 are $h_2 = 0.4, 0.5, 0.8$, respectively for panels (a), (b), (c) in Figure 6 and Figure 7. Comparing the graphs, we observe similar time-evolution behaviors among these three species! This means that when the competition effect of the catfish is at least as strong as the striped bass $\alpha \geq \beta$, the bass loses and dies out even when harvesting of the catfish happens up to a certain point.

Panel (d) in Figure 7 illustrates a very different scenario. When the competition strength between the striped bass and the catfish are equal, and when the harvesting rate $h_2 = 1.2 > 0.5 = e$ is big enough, the model shows that catfish can be driven to extinction while the menhaden and striped bass persist with a regular predator-prey relationship.

In conclusion, this model predicts the extinction of one of the two predators depending on their competitiveness. These results are consistent with the fundamental ecological principle of competitive exclusion, also called the Gause principle, which states that when two competing species that attempt to occupy the same niche in an ecosystem can not co-exist indefinitely, one population will either go extinct or will adapt to fill a different niche [4].

7 Writing and assessment of the project

Preparing a mathematical report is an important skill for STEM students. The report must be accurate, well-structured, and thorough, must look professional, and must not be presented like a typical homework assignment that students complete on a daily basis. The readers of the report and the audience of the presentation should be able to understand the report without being burdened by mathematical computations. It can even be said that creating the report is almost as important as the analysis that goes into the process of creating the model and solving the problem.

In this section, we include suggestions on how the mathematical report may be prepared by students and how their work may be assessed by a grading rubric.

Mathematical report

The mathematical report may be divided into the following sections:

Figure 7: Menhaden, striped bass, and catfish population distributions over time when a linear harvesting term $-h_2 z$ of the blue catfish is included in the model. The following values of the parameters were used: $a = d = e = 0.5$, $b = c = 0.01$, $\alpha = \beta = 0.5$ with initial conditions $(100, 10, 10)$. Panels (a) $h_2 = 0.4$, (b) $h_2 = 0.5$, (c) $h_2 = 0.8$, (d) $h_2 = 1.2$.

1. **Statement of the problem and existing data.** This section contains the natural phenomenon being studied, the significance of the project, and all existing qualitative and quantitative data.
2. **Mathematical model.** This section identifies the variables, the parameters, and the differential equations used to model the problem. It also contains the assumptions and the rationale for them. It should explain each component of the differential equations.
3. **Mathematical analysis.** This section contains some mathematical computations that lead to the specific answers to the questions or scenarios proposed in the given problem. Computational steps may be skipped if necessary, but every key step must be explained.
4. **Numerical simulations.** This section contains the numerical discoveries and analysis through visualizations. The graphs should be explained clearly.
5. **Conclusions.** This section summarizes the final results. It should contain the answers to the motivating problem, and it must be presented in the language that is relevant to the phenomenon being studied.

When presented to clients or to an audience who are not necessarily mathematically-trained in differential equations, the project must be presented in a language that can be understood. The report may have informal language to help develop intuition and understanding.

Grading rubric

The students' work on this project may be graded with respect to the following tasks:

1. Describe the observed phenomenon in Chesapeake Bay as reported in media, websites by environmental agencies, and/or government offices.
2. Enumerate and distinguish assumptions and simplifications.
3. Define the variables and parameters. Create the system of ordinary differential equations.
4. Solve for the equilibrium points. Analyze the linear stability of each equilibrium point.
5. Create time-evolutions and phase portraits using a numerical and visualization software such as MATLAB.
6. Interpret theoretical results, graphical simulations, and numerical computations.

8 Conclusion

Inquiry-based projects enable students to actively discover information while the instructor guides students through posing research questions, designing methods, and interpreting data with the main goal of helping students develop critical thinking and deeper understanding of the material. In this paper, we present an inquiry-based project that is designed for a mathematical modeling class of undergraduate junior or senior students. This project discusses a three-species mathematical model that simulates the biological interactions among three important fish species in the Chesapeake Bay: the prey Atlantic menhaden and its two competing predators: the striped bass and the blue catfish. The model also considers the following ecological issues related to these three species: the overfishing of menhaden, the invasiveness of the blue catfish, and the harvesting of blue catfish as a method to control the population. This model builds naturally upon the classical Lotka-Volterra prey-predator models and allows students to apply their theoretical knowledge from previous classes in calculus, linear algebra, and differential equations for investigating real-world ecological problems.

We use a series of modified modeling scenarios based on some simplifying assumptions to demonstrate the application of theoretical concepts to actual fisheries in the Chesapeake Bay. We start with a three-species system (B) including prey menhaden $x(t)$ and two competing predators striped bass $y(t)$ and blue catfish $z(t)$ and assume no harvesting effect and equal competition interference between y and z . Then we build this system up by including harvesting terms on the menhaden (C) and harvesting terms on the catfish (D). Then we consider a case when competition interference is not equal (E) and finally, a system that has unequal competition with overfishing of the catfish (F).

To study the local stability of the equilibrium points to non-linear systems of differential equations, the linearization theory and the Hartman-Grobman theorem were used through algebraic, analytic, and numerical methods. In particular, when solving the characteristic equation was not straight-forward, the Routh-Hurwitz criteria was applied. It was found that even though the co-existence equilibrium (when all three species exist together), is possible if $\alpha > \alpha_{\text{crit}}$ for some critical value $\alpha_{\text{crit}} = (cd + be)/a$, this equilibrium is highly unstable. If one species exceeds its critical size or fails to achieve it, then the model predicts that at least one species will die out.

Numerical simulations via MATLAB were utilized to study the long-term behavior of the three fish population dynamics. All three case scenarios representing the competitiveness between the two predators $\alpha < \beta$, $\alpha = \beta$, and $\alpha > \beta$ were analyzed. The model shows that in the long run if $\alpha = \beta$ (or the two predators are equally competitive), the catfish, as an invasive species, would persist while the menhaden and the striped bass would become extinct. If the catfish is assumed to be less competitive, or the case $\alpha < \beta$, then catfish become extinct while the menhaden and the striped bass co-exist with the typical phase-shifted periodic behavior. The model shows that this is the only scenario in which striped bass could survive. However, in reality, the catfish is much more competitive ($\alpha > \beta$) as it preys on a variety of fish and makes up almost 75 percent of all fish biomass in the Chesapeake Bay's fisheries. Hence, the model predicts the unlimited growth of the catfish and the extinction of both native species: the menhaden and the striped bass.

The model shows that linear harvesting is sufficient to limit the growth of the invasive

catfish population, provided that the competition between the striped bass and the catfish is strong enough. Moreover, if the harvesting coefficient is sufficiently large, it is possible for the catfish and the menhaden to co-exist with phase-shifted periodic behavior but the striped bass becomes extinct.

In either case, the model predicts extinction of one of the two predators depending on their competitiveness. These results illustrate the fundamental ecological principle of competitive exclusion according to which two competing species that attempt to occupy the same niche in an ecosystem cannot co-exist indefinitely and one of the two populations will either go extinct or will adapt to fill a different niche.

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