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Abstract: We consider a three-species fish dynamical system in Chesapeake Bay consisting of the Atlantic menhaden as the prey and its two competing predators, the striped bass and the catfish. Building on our previous work in this system, we consider the issue of balancing economic harvesting goals (financial gain for fishermen) with ecological harvesting goals (non-extinction of species). In particular, we investigate the bionomic equilibria, maximum sustainable yield, and the maximum economic yield. Analytical computations and numerical simulations are employed to provide some mathematical guidance on fisheries management policies.

1 Introduction

Chesapeake Bay, located in the Mid-Atlantic region, is the largest estuary in the United States and is home to hundreds of species of fish. Commmercial and recreational fishing are significant drivers of the economy in this region and several local government agencies manage fisheries in the Chesapeake Bay, including the Maryland Department of Natural Resources, Virginia Marine Resources Commission, and the Potomac River Fisheries Commission [9]. Along with the National Oceanic and Atmospheric Administration (NOAA), these agencies create "ecosystem-based fishery management" in order to "sustainably manage the nation's marine fisheries" [9].

Recently, a fishing management strategy has been developed by NOAA and its local partner agencies to examine the potential impacts of commercial and recreational harvesting of one of Chesapeake Bay's species, the blue catfish, as "a means to reduce their abundance and mitigate their range expansion and ecological impacts" [7, 1]. NOAA has reported that this particular fish species is an invasive species in the Chesapeake Bay. As a result, this agency has recommended various strategies to control the spread of the blue catfish, to include consumer-level management programs that promote harvesting and eating the invasive species.

Harvesting any fish species, however, must consider its social, ecological, and economic effects. It is important to balance and manage the population size of fish species (ecological), the revenues/costs/profits of fishing (economics), the amount of fishing effort and jobs (social), and the provision of food for people (social). In this paper, we will only consider the problem of managing the ecological and economic harvesting goals in a specific three-species system in Chesapeake Bay using ordinary differential equations. Mathematically investigating the ecological, economic, and social impacts of over-harvesting may require a combination of dynamical system techniques, network analysis methods, and statistical perspectives.

In 1954, Schaefer [13] suggested and justified that a single species fishery will achieve maximum sustainable yield (MSY) and maximum economic yield (MEY), assuming logistic growth on the fish species. Maximum sustainable yield is the highest possible harvesting level at which a species may be harvested without the risk of extinction over time. Maximum economic yield is the highest possible harvesting level that provides maximum economic benefits over time. Balancing ecological and economic goals by computing and analyzing the MSY and MEY in fishery systems provides important theoretical insights that guide public policies on managing fisheries. Intuitively, it is relatively easy to understand that over-fishing at extreme levels in a short period of time may quickly result to depletion and extinction of fish species. However, it may not be apparent that harvesting beyond a certain level may not necessarily result to more economic gains, for example, higher profits for the fishermen.

Later, Legovic [5] showed that harvesting of the prey at the MSY level in a predator-prey system might result in the extinction of the predator, due to the reduced source of food supply. As a result, any management policy must consider the interactions between species when deciding on harvesting quotes, as the population dynamics between species is inevitably linked. Hence, it is not clear whether a direct application of MSY theory toward one species, such as the invasive blue catfish, would be sustainable for the whole ecosystem. Further research on the intricate ecological and economic dynamics between the predator and prey is needed. Mathematical modeling via differential equations provides a method to simulate the dynamics of growth, death, competition, interaction, harvesting, with some economic considerations.

Fisheries management is often done as one-species management and is focused on maximizing the yield of this targeted species ignoring the inter-species interactions or any other ecosystem effects. Such one-dimensional policy often leads to deterioration of the stocks and in the case of Atlantic menhaden has already resulted in critical decrease of the menhaden's population in the Bay area [2]. Only recently, the Atlantic States Marine Fisheries Commission (ASMFC) has taken the first step to formally consider the importance of one species to others, particularly the importance of menhaden to other predators, including the striped bass. In their new management policy, they committed to including ecological reference points on menhaden's population and reduced the harvesting quota on menhaden by 10 percent for 2021 and 2022 fishing seasons [3].

This article builds upon the previous work [11] of the authors on three important species in the Chesapeake Bay, involving the Atlantic menhaden as the prey to two competing predators, the striped bass and the blue catfish (Figure 1).

(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: Pictures from Chesapeake Bay Program, `www.chesapeakebay.net`.

In [11], a mathematical model was built from a Lotka-Volterra model with the following assumptions: exponential growth on the menhaden, dependence of bass on the menhaden, competition between the bass and catfish, and exponential growth on the catfish. The reasoning behind the exponential growth assumption for the catfish is the fact that this fish is an invasive fish in the Bay and is a generalist predator, meaning that it does not depend on menhaden only as a prey. In the absence of menhaden, it can prey on many other species and as a result the catfish population is increasing very fast and currently, they make up about 75 percent of the biomass in the Chesapeake Bay area [8, 10].

Here, we continue the study of the three-species model we introduced in [11] with the aim of balancing ecological and economic harvesting goals. 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. logistic growth on prey x (menhaden),
2. the two predators y (bass) and z (catfish) are in competition, both preying on x,
3. the predator y declines at a rate proportional to its size in the absence of x, and
4. the predator z is an invasive species and grows exponentially at a rate proportional to its size.

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

$$\begin{cases} x' &= ax(1 - x/K) - bxy - cxz \\ y' &= -dy + bxy - \alpha yz \\ z' &= ez + cxz - \beta yz. \end{cases} \tag{A}$$

with initial data values $x(0) \geq 0, y(0) \geq 0, z(0) \geq 0$. The parameters are in Table 1.

a	growth parameter of x
b	preying effect of y on x
c	preying effect of z on x
d	death parameter of the predator y
e	growth parameter of z
K	environmental carrying capacity of x
α	competition effect of z on y
β	competition effect of y on z

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

The paper is organized as follows. In Section 2, we investigate the bio-economic equilibria (also known as bionomic equilibria) of the system and derive conditions for their existence. A bionomic equilibrium is a point that considers not only the biological or ecological equilibrium, but also the economic equilibrium, with the latter being investigated using a profit analysis technique from Economics. In Section 3, we compute conditions for MSY policy in order to guarantee that none of our three species become extinct. Numerically-simulated graphs are presented to aid analysis and discussion. In Section 4, we look at the issue of balancing economic and ecological harvesting goals.

2 Bionomic Equilibrium

Bionomic equilibrium comes from biological equilibrium and economic equilibrium. Biological equilibrium is attained when $x' = y' = z' = 0$ while economic equilibrium is attained when total revenue earned by selling the harvested biomass is equal to the total cost for the effort in harvesting the biomass. The idea comes from [12] and [14].

The goal of this section is to find conditions under which bionomic equilibria exist. Toward this goal, we look at a way to measure the overall net revenue by adding the net revenue for each of our three fish species. The overall net revenue, also known as economic rent (or even profit), of the dynamical system involves parameters on cost per unit effort, price per unit, and catchability coefficient for each of the three species (see Table 2):

$$\pi(t) = (p_1 q_1 x(t) - c_1)E_1 + (p_2 q_2 y(t) - c_2)E_2 + (p_3 q_3 z(t) - c_3)E_3,$$

at any given time t where E_1, E_2, E_3 are the harvesting effort coefficients of the Atlantic menhaden, the striped bass, and the catfish, respectively.

Thus, we need to consider the dynamical system

$$\begin{cases} x' &= ax(1 - x/K) - bxy - cxz - q_1 E_1 x \\ y' &= -dy + bxy - \alpha yz - q_2 E_2 y \\ z' &= ez + cxz - \beta yz - q_3 E_3 z \\ \pi &= (p_1 q_1 x - c_1)E_1 + (p_2 q_2 y - c_2)E_2 + (p_3 q_3 z - c_3)E_3 \end{cases} \tag{B}$$

c_1	fishing cost per unit effort for Atlantic menhaden
c_2	fishing cost per unit effort for striped bass
c_3	fishing cost per unit effort for catfish
p_1	price per unit biomass of Atlantic menhaden
p_2	price per unit biomass of striped bass
p_3	price per unit biomass of catfish
q_1	catchability coefficient of Atlantic menhaden
q_2	catchability coefficient of striped bass
q_3	catchability coefficient of catfish

Table 2: The economic parameters in model (B). All parameters are positive.

with initial data values $x(0) \geq 0, y(0) \geq 0, z(0) \geq 0$. In other words, conditions on the existence of bionomic equilibria can be obtained by solving the system

$$\begin{cases} a(1 - x/K) - by - cz - q_1E_1 &= 0 \\ -d + bx - \alpha z - q_2E_2 &= 0 \\ e + cx - \beta y - q_3E_3 &= 0 \\ (p_1q_1x - c_1)E_1 + (p_2q_2y - c_2)E_2 + (p_3q_3z - c_3)E_3 &= 0. \end{cases} \tag{2.1}$$

Observe that we did not consider the biological equilibrium $E_0(x, y, z) = (0, 0, 0)$ because in this case, the overall net revenue π becomes negative. Also, we focus on the biologically relevant interior equilibria with $x, y, z \neq 0$. Observe that the bionomic equilibrium P is characterized not only by x, y, z but also by E_1, E_2, E_3

Suppose the bionomic equilibria is $P(x_B, y_B, z_B, E_1, E_2, E_3)$. In order for all equations to be satisfied at P, we need to consider eight cases. Full details of the proofs for Cases 1 and 2 are given; proofs for the other cases are similar.

Case 1. No harvesting efforts on the prey.

In this case, we have that $E_1 = 0$ and both E_2 and E_3 are positive, that is, the Atlantic menhaden is not harvested but the striped bass and the catfish are both harvested. We assume that the decision to harvest both predators rely on the fact that net revenue for each of the predators is non-negative. In other words, it does not make sense, economically speaking, to harvest the striped bass if the cost c_2 to harvest them is higher than the price p_2q_2y earned by selling them; similarly, we want $c_3 \leq p_3q_3z$. Thus, we take $y_B = \frac{c_2}{p_2q_2}$ and $z_B = \frac{c_3}{p_3q_3}$. These conditions on E_1, y_B, and z_B guarantee that the fourth equation in (2.1) is equal to zero.

Computing the harvesting effort coefficients E_2 and E_3 of the striped bass and the catfish, respectively, from the second and third equations in (2.1) we get:

$$E_2 = \frac{bx_B}{q_2} - \frac{d}{q_2} - \frac{\alpha}{q_2}\frac{c_3}{p_3q_3} \text{ and } E_3 = \frac{cx_B}{q_3} + \frac{e}{q_3} - \frac{\beta}{q_3}\frac{c_2}{p_2q_2}. \tag{2.2}$$

Since we want the harvesting efforts E_2 and E_3 to be positive, we solve for x_B from both equations in (2.2) to obtain:

$$x_B > \frac{d}{b} + \frac{\alpha}{b}\frac{c_3}{p_3 q_3} \text{ and } x_B > \frac{-e}{c} + \frac{\beta}{c}\frac{c_2}{p_2 q_2}. \tag{2.3}$$

Now, using the first equation in (2.1), we obtain an explicit expression for x_B:

$$x_B = K\left(1 - \frac{b}{a}\frac{c_2}{p_2 q_2} - \frac{c}{a}\frac{c_3}{p_3 q_3}\right). \tag{2.4}$$

The biologically relevant case is when $x_B > 0$, hence, $1 - \frac{b}{a}\frac{c_2}{p_2 q_2} - \frac{c}{a}\frac{c_3}{p_3 q_3} > 0$. Putting together the conditions (2.3) and (2.4), we have

$$K\left(1 - \frac{b}{a}\frac{c_2}{p_2 q_2} - \frac{c}{a}\frac{c_3}{p_3 q_3}\right) > \frac{d}{b} + \frac{\alpha c_3}{b p_3 q_3} \text{ and } K\left(1 - \frac{b}{a}\frac{c_2}{p_2 q_2} - \frac{c}{a}\frac{c_3}{p_3 q_3}\right) > -\frac{e}{c} + \frac{\beta c_2}{c p_2 q_2}.$$

that is,

$$K > \frac{d}{b} + \frac{\alpha c_3}{b p_3 q_3} \text{ and } K > -\frac{e}{c} + \frac{\beta c_2}{c p_2 q_2}.$$

These conditions on the carrying capacity K of the prey x determine the existence of the bionomic equilibrium P for Case 1:

Theorem 2.1. *Assume that* $1 - \frac{b}{a}\frac{c_2}{p_2 q_2} - \frac{c}{a}\frac{c_3}{p_3 q_3} > 0$. *Suppose* K *is chosen such that*

$$K > \max\left\{\frac{d}{b} + \frac{\alpha c_3}{b p_3 q_3}, \quad -\frac{e}{c} + \frac{\beta c_2}{c p_2 q_2}\right\}.$$

When there are no harvesting efforts on the prey, the bionomic equilibrium $P\,(x_B, y_B, z_B, 0, E_2, E_3)$ *exists, where* x_B *is given by (2.4),* $y_B = \frac{c_2}{p_2 q_2}$, $z_B = \frac{c_3}{p_3 q_3}$ *and the harvesting efforts on the predators are given by (2.2).*

Case 2. No harvesting efforts on first predator.

In this case, we have that $E_2 = 0$ while both E_1, E_3 are positive, that is, the Atlantic menhaden and the catfish are both harvested. To find the bionomic equilibrium $P(x_B, y_B, z_B, E_1, 0, E_3)$, as in the previous case, we assume that $x_B = \frac{c_1}{p_1 q_1}$ and $z_B = \frac{c_3}{p_3 q_3}$.

We solve for E_1 and E_3 from the first and third equations of (2.1) to get

$$E_1 = \frac{a}{q_1}\left(1 - \frac{c_1}{p_1 q_1 K}\right) - \frac{b}{q_1} y_B - \frac{c}{q_1}\frac{c_3}{p_3 q_3} \text{ and } E_3 = \frac{e}{q_3} + \frac{c}{q_3}\frac{c_1}{p_1 q_1} - \frac{\beta}{q_3} y_B. \tag{2.5}$$

Now, our conditions on the existence of the bionomic equilibrium requires finding a minimum, not a maximum like in the previous case. This is because the population growth of the first predator y declines in the absence of x. Moreover, using the second equation in (2.1), we have a condition on the parameter d:

$$d = b\frac{c_1}{p_1 q_1} - \alpha\frac{c_3}{p_3 q_3}.$$

Observe that unlike the previous case, we do not have an explicit expression for y_B but we have a condition on its death parameter d. Upon requiring that both E_1 and E_3 are positive, we have now proved:

Theorem 2.2. *Assume $d = b\frac{c_1}{p_1 q_1} - \alpha\frac{c_3}{p_3 q_3} > 0$. Suppose y_B is chosen such that*

$$0 < y_B < \min\left\{\frac{a}{b}\left(1 - \frac{c_1}{p_1 q_1 K}\right) - \frac{c}{b}\frac{c_3}{p_3 q_3}, \quad \frac{e}{\beta} + \frac{c}{\beta}\frac{c_1}{p_1 q_1}\right\}.$$

When there are no harvesting efforts on the first predator, the bionomic equilibrium $P\left(x_B, y_B, z_B, E_1, 0, E_3\right)$ exists, where $x_B = \frac{c_1}{p_1 q_1}$, $z_B = \frac{c_3}{p_3 q_3}$, and the harvesting efforts on the prey and the second predator are given in (2.5).

Case 3. No harvesting efforts on second predator.

Here $E_3 = 0$ and $x_B = \frac{c_1}{p_1 q_1}$ and $y_B = \frac{c_2}{p_2 q_2}$.

Theorem 2.3. *Assume $e = \beta\frac{c_2}{p_2 q_2} - c\frac{c_1}{p_1 q_1} > 0$. Suppose z_B is chosen such that*

$$0 < z_B < \min\left\{\frac{a}{c}\left(1 - \frac{c_1}{p_1 q_1 K}\right) - \frac{b}{c}\frac{c_2}{p_2 q_2}, \quad \frac{-d}{\alpha} + \frac{b}{\alpha}\frac{c_1}{p_1 q_1}\right\}$$

When there are no harvesting efforts on the second predator, the bionomic equilibrium $P\left(x_B, y_B, z_B, E_1, E_2, 0\right)$ exists where $x_B = \frac{c_1}{p_1 q_1}$, $y_B = \frac{c_2}{p_2 q_2}$ and the harvesting efforts on the prey and the first predator are given by

$$E_1 = \frac{a}{q_1}\left(1 - \frac{c_1}{p_1 q_1 K}\right) - \frac{b}{q_1}\frac{c_2}{p_2 q_2} - \frac{c}{q_1} z_B \text{ and } E_2 = \frac{-d}{q_2} + \frac{b}{q_2}\frac{c_1}{p_1 q_1} - \frac{\alpha}{q_2} z_B.$$

There are five more cases to consider. Unlike Cases 2 and 3, these remaining cases have exact expressions for all components of the bionomic equilibrium $P(x_B, y_B, z_B, E_1, E_2, E_3)$. We need to require that each component of P is positive in order to insure that P exists.

> *Student Exploration Activity.* There are eight cases to consider when analyzing the bionomic equilibria in different harvesting scenarios. Three of the cases were explicitly computed in the discussion. Look at the other five cases: verify that that the components of the bionomic equilibria are as listed in Table 3.

3 Maximum Sustainable Yield

Analyzing the maximum sustainable yield (MSY) is one of the scientific approaches in managing harvesting and fishing efforts. It balances over-exploitation and under-exploitation, where over-exploitation involves harvesting a resource at a level that threatens its extinction while under-exploitation is the harvesting of a resource that is below the level that the population can withstand.

Computing the bionomic equilibria$(x_B, y_B, z_B, E_1, E_2 E_3)$in different harvesting scenarios.
Case 4. No harvesting efforts on the prey and the first predator. $E_1 = E_2 = 0,\;\; E_3 = \frac{1}{q_3}(e + cx_B - \beta y_B)$ $(x_B, y_B, z_B) = (\frac{1}{b}(d + \alpha z_B), \frac{1}{b}(a(1 - \frac{x_B}{K}) - cz_B), \frac{c_3}{p_3 q_3})$
Case 5. No harvesting efforts on the prey and the second predator. $E_1 = E_3 = 0,\;\; E_2 = \frac{1}{q_2}(-d + bx_B - \alpha y_B)$ $(x_B, y_B, z_B) = (\frac{1}{c}(-e + \beta y_B), \frac{c_2}{p_2 q_2}, \frac{1}{c}a(1 - \frac{x-B}{K}) - by_B)$
Case 6. No harvesting efforts on both predators. $E_2 = E_3 = 0,\;\; E_1 = \frac{1}{q_1}(a(1 - \frac{x_B}{K}) - by_B - cz_B)$ $(\frac{c_1}{p_1 q_1}, \frac{1}{b}(e + cx_B), \frac{1}{\alpha}(-d + bx_B))$
Case 7. No harvesting efforts on all species. $E_1 = E_2 = E_3 = 0$ $(x_B, y_B, z_B) = (\frac{1}{M}(cd\beta + a\alpha\beta - be\alpha), \frac{1}{M}(ac\alpha + bce + c^2 d + \frac{ae\alpha}{K}), \frac{1}{M}(ab\beta - \frac{ad\beta}{K} - bcd - b^2 e)$
Case 8. Harvesting all species. $E_1 = \frac{1}{q_1}(a(1 - \frac{x_B}{K}) - by_B - cz_B), E_2 = \frac{1}{q_2}(-d + bx_B - \alpha y_B), E_3 = \frac{1}{q_3}(e + cx_B - \beta y_B)$ $(x_B, y_B, z_B) = (\frac{c_1}{p_1 q_1}, \frac{c_2}{p_2 q_2}, \frac{c_3}{p_3 q_3})$

Table 3: The table summarizes the bionomic equilibria on each harvesting scenario. Cases 1, 2, 3 are discussed in the text.

The ecological issue that we need to check is extinction of any of our three species when harvesting is implemented. Thus, from the original system (A), we consider the dynamical system

$$\begin{cases} x' &=& ax(1 - x/K) - bxy - cxz - E_1 x \\ y' &=& -dy + bxy - \alpha yz - E_2 y \\ z' &=& ez + cxz - \beta yz - E_3 z. \end{cases} \tag{C}$$

with initial data values $x(0) \geq 0, y(0) \geq 0, z(0) \geq 0$. To compute the MSY, we look at the harvesting yield as a function of the harvesting effort. We consider several relevant cases: harvesting of the Atlantic menhaden only (that is, no harvesting efforts on the two predators so that $E_2 = E_3 = 0$), harvesting of the striped bass and catfish only ($E_1 = 0$), and the special case of harvesting the catfish only ($E_1 = E_2 = 0$). Analysis of the other cases follows analogous arguments. We start by looking at the equilibrium of (C) and considering the interior cases only. Observe that, ecologically, we interpret any of the cases $x = 0$, $y = 0$, $z = 0$ to mean extinction of the corresponding species. Hence, consider the system:

$$\begin{cases} a(1 - x/K) - by - cz - E_1 &=& 0 \\ -d + bx - \alpha z - E_2 &=& 0 \\ e + cx - \beta y - E_3 &=& 0 \end{cases} \tag{3.1}$$

Harvesting Prey Only.

In this case, take $E_2 = E_3 = 0$ and solve for x, y, z as functions of $E = E_1$ in (3.1). Suppose $M = \frac{a}{K}\alpha\beta + bc(\alpha+\beta)$. We have:

$$x(E) = \frac{1}{M}\left(-\alpha\beta E + cd\beta + a\alpha\beta - be\alpha\right) \quad y(E) = \frac{c}{\beta}x(E) + \frac{e}{\beta}, \quad z(E) = \frac{b}{\alpha}x(E) - \frac{d}{\alpha}$$

Let us denote the slope of $x(E)$ by m_x, that is, write $x(E) = m_x E + x(0)$ where

$$m_x = \frac{-\alpha\beta}{M}, \quad x(0) = \frac{cd\beta + a\alpha\beta - be\alpha}{M}.$$

Note that the biologically relevant scenario is the case when $x(0) > 0$. Also, we observe that $\frac{dx}{dE} = m_x < 0$. Since $\frac{dy}{dE}$ and $\frac{dz}{dE}$ are also negative, we see that an increase in harvesting efforts of the prey will result to a decrease in the biomass of all three fish species.

As an example of how to interpret the results so far from the ecological perspective, suppose, for instance, that the competition between the two predators are unequal with the second predator more aggressive than the first (that is, $\alpha > \beta$) and suppose that the preying effect of either predators on the prey are the same (that is, $b = c$). Then the biomass of the first predator decreases faster than the biomass of the second predator (that is, $dy/dE < dz/dE$) due to the harvesting of the prey and the competition between the predators.

Now, the yield function $Y(E)$ in this case is defined as $Y(E) = Ex(E)$. Since $x(E)$ is a linear function, $Y(E)$ is a quadratic function of E that achieves a maximum yield at the effort E given by

$$E^* = \frac{-x(0)}{2m_x} = \frac{cd\beta + a\alpha\beta - be\alpha}{2\alpha\beta}, \tag{3.2}$$

which is one-half of the E-intercept of $x(E)$. Denote

$$E_y^* = \frac{-cx(0) - e}{cm_x} = \frac{ac\alpha + bce + +c^2d + \frac{a}{K}e\alpha}{c\alpha} \text{ and } E_z^* = \frac{-bx(0) + d}{bm_x} = \frac{-ab\beta + \frac{ad}{K}\beta + bcd + b^2e}{-b\beta}, \tag{3.3}$$

which are the E-intercepts of the linear functions $y(E)$ and $z(E)$. In other words, at these harvesting efforts, the biomasses for the species y and z are zero and hence, the predators are considered extinct ($y = 0 = z$).

Theorem 3.1. *Assume that $cd\beta + a\alpha\beta - be\alpha > 0$. When harvesting the prey only, maximum sustainable yield is achieved, provided*

$$E^* < \min\left\{E_y^*, E_z^*\right\},$$

where E^*, E_y^*, E_z^* are given in (3.2) and (3.3).

A graphical illustration of the ideas will provide context to Theorem 3.1. In Figure 2, the yield function $Y(E) = Ex(E)$ is a parabola that has a highest point because $x(E)$ is a linear function with negative slope. Observe that $y(E), z(E)$ are also linear functions with negative slopes. The maximum sustainable yield E^* is the E-coordinate of the highest point of the yield function. Maximum sustainability in harvesting all three species is attained when harvesting effort E^* on the prey only is to the left of the points E^*_Y and E^*_Z. In other words, one has to insure that harvesting the prey x only should occur before y and z become extinct.

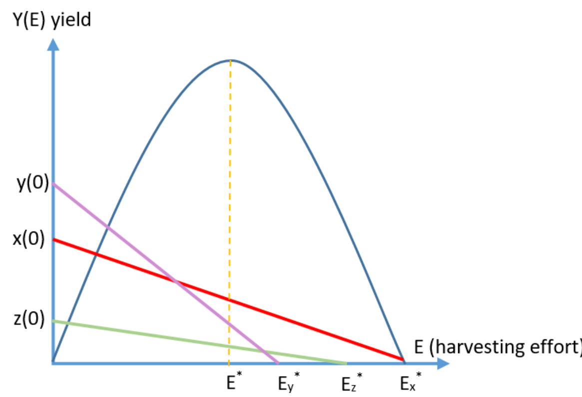


Figure 2: A graph of the yield function $Y(E) = Ex(E)$ with the populations $x(E), y(E), z(E)$ as functions of the harvesting effort E when harvesting the prey only. Maximum sustainable yield is achieved provided that harvesting is implemented before any of the three populations become extinct.

Theorem (3.1) implies that

- If $E^* > E^*_y$ then harvesting prey only at effort E^* causes extinction of the first predator,
- if $E^* > E^*_z$ then harvesting prey only at effort E^* causes the extinction of the second predator, and
- if $E^* > max\{E^*_y, E^*_z\}$ then harvesting prey only at effort E^* causes the extinction of both predators.

Choosing particular values for the model's parameters $K = 1, a = 1, b = 0.2, c = 0.01, d = 0.01, e = 0.05$ and assuming that the catfish is more competitive than the bass, i.e. $\alpha = 0.8$, and $\beta = 0.5$, we can plot the yield function and the biomass of the three fish with respect to the harvesting effort as shown in Figure 3. As we can see from the graph, in this particular case harvesting the prey only at MSY level is sustainable and does not lead any one of the three species to extinction.

Harvesting Predators Only.

In this case, take $E_1 = 0$ and solve for x, y, z. For simplicity, assume $E_2 = E_3 = E$. Suppose $M = \frac{a}{K}\alpha\beta + bc(\alpha + \beta)$. We obtain

$$x(E) = \frac{1}{M}\left((b\alpha + c\beta)E + a\alpha\beta - be\alpha + cd\beta\right),$$

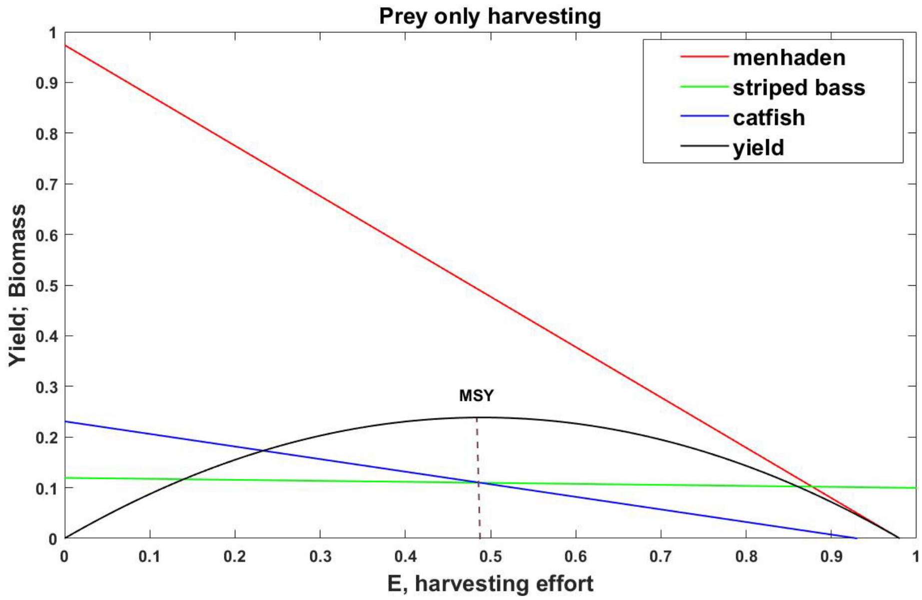


Figure 3: Yield and the three species biomass as a function of the harvesting effort when harvesting the prey only. Parameters values are as follows: $K = 1, a = 1, b = 0.2, c = 0.01, d = 0.01, e = 0.05, \alpha = 0.8$, and $\beta = 0.5$.

$$y(E) = \frac{c}{\beta}x(E) + \frac{e-E}{\beta}, \quad z(E) = \frac{b}{\alpha}x(E) - \frac{d+E}{\alpha},$$

which are linear functions on E. Let us denote the slope of $x(E)$ by m_x so that $x(E) = m_x E + x(0)$. The biologically relevant scenario is the case when $x(0) > 0$.

Observe that $\frac{dx}{dE} > 0$ so that increasing the harvesting efforts on the predators does not result to a decrease in the biomass of the prey. Note that

$$\frac{dy}{dE} = \frac{1}{\beta}(cm_x - 1) \quad \text{and} \quad \frac{dz}{dE} = \frac{1}{\alpha}(bm_x - 1).$$

Theorem 3.2. *Suppose $m_x > \max\{\frac{1}{b}, \frac{1}{c}\}$. Then both $\dfrac{dy}{dE}$ and $\dfrac{dz}{dE}$ are positive.*

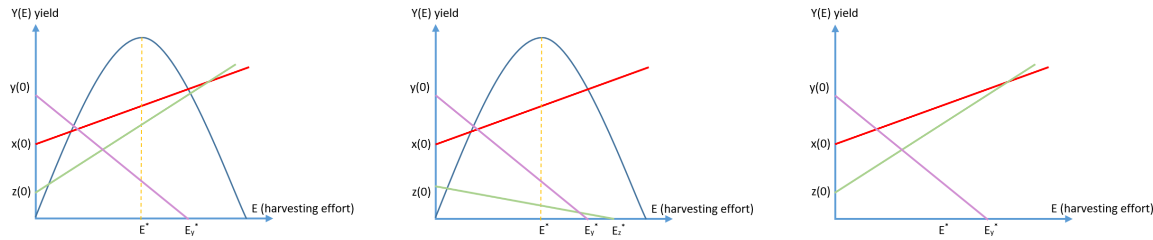
The theorem implies that when conditions on m_x are as stated, then increasing the harvesting efforts on the predators will not result to a decrease in the biomass of either predator.

To analyze the situation where either $\frac{dy}{dE}$ or $\frac{dz}{dE}$ is negative, let us now consider the yield function when harvesting the predators (quadratic function):

$$Y(E) = E(y(E) + z(E)),$$

or, upon re-arranging, we have

$$Y(E) = E\left(\left(\left(\frac{c}{\beta} + \frac{b}{\alpha}\right)m_x - \frac{1}{\beta} - \frac{1}{\alpha}\right)E + \left(\frac{c}{\beta} + \frac{b}{\alpha}\right)x(0) + \frac{e}{\beta} - \frac{d}{\alpha}\right).$$



(a) $Y(E) = E(y(E) + z(E))$ when $y'(E) < 0 < z'(E)$

(b) $Y(E) = E(y(E) + z(E))$ when both $y'(E), z'(E) < 0$

(c) $Y(E) = Ez(E)$, yield has no maximum

Figure 4: When harvesting both predators, the yield function is represented by a parabola that has a maximum. When harvesting the second predator only, the yield function is represented by a parabola that does not have a maximum because $z'(E) > 0$.

In order to have a maximum yield, we must require that the parabola opens downward, that is

$$\left(\frac{c}{\beta} + \frac{b}{\alpha}\right) m_x - \frac{1}{\beta} - \frac{1}{\alpha} < 0 \iff (c\alpha + b\beta)m_x - \alpha - \beta < 0.$$

The maximum yield occurs when the harvesting effort E is

$$E^* = \frac{-1}{2} \frac{(c\alpha + b\beta)x(0) + e\alpha - d\beta}{(c\alpha + b\beta)m_x - \alpha - \beta}, \tag{3.4}$$

where, in order for E^* to be positive, we must also require that $(c\alpha + b\beta)x(0) + e\alpha - d\beta > 0$. Denote

$$E_y^* = \frac{-e - cx(0)}{cm_x - 1} \text{ and } E_z^* = \frac{d - bx(0)}{bm_x - 1}. \tag{3.5}$$

Observe that $E_y^* > 0$ provided $cm_x - 1 < 0$. This implies that $\frac{dy}{dE}$ is always negative. In order for E_z^* to be positive, we must consider two cases: $bm_x - 1 < 0$ and $d - bx(0) < 0$, or, $bm_x - 1 > 0$ and $d - bx(0) > 0$. In the previous case, $m_x < 1/b$ so that $\frac{dz}{dE}$ is negative or that the biomass of z decreases with increasing harvesting efforts on z. In the latter, $\frac{dz}{dE}$ is positive, which tells us that even though we are harvesting z, it is still possible that its biomass continues to increase. Illustrations of the different scenarios are given in Figure 4 and a numerically simulated graph is given in Figure 5. When both predators are harvested at MSY level, the system is sustainable, even though the biomass of the striped bass gets critically low, while the biomass of the prey (menhaden) is increasing.

Theorem 3.3. *Assume that $(c\alpha + b\beta)m_x - \alpha - \beta < 0$ and $(c\alpha + b\beta)x(0) + e\alpha - d\beta > 0$. Then*

- *Suppose $dy/dE < 0 < dz/dE$. When harvesting the predators, maximum sustainable yield is achieved, provided*
$$E_z^* < E^* < E_y^*,$$
- *suppose $dy/dE < 0$ and $dz/dE < 0$. When harvesting the predators, maximum sustainable yield is achieved, provided*
$$E^* < \min\{E_y^*, E_z^*\},$$
where E^*, E_y^*, E_z^* are given in (3.4) and (3.5).

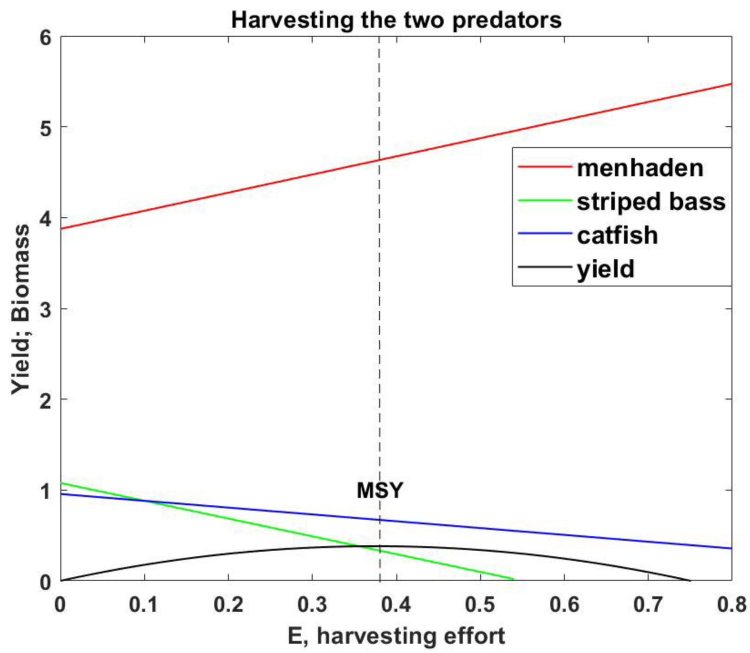


Figure 5: Yield and the three species biomass as a function of the harvesting effort when harvesting both predators. Parameters values are as follows: $K = 5, a = 1, b = 0.2, c = 0.01, d = 0.01, e = 0.5, \alpha = 0.8$, and $\beta = 0.5$.

Harvesting the Second Predator Only.

In the special case that only the second predator is harvested, we continue the discussion from above but this time we have $E_1 = E_2 = 0$ and $E_3 = E$. Then the corresponding linear functions for the biomasses x, y, z as functions of the harvesting effort E are:

$$\begin{array}{rcl} x(E) & = & \frac{1}{M}(b\alpha E + cd\beta + a\alpha\beta - be\alpha), \\ y(E) & = & \frac{1}{M}\left((\frac{-a}{K}\alpha - bc)E + ac\alpha + bce + c^2 d + \frac{a}{K}e\alpha\right) \\ z(E) & = & \frac{1}{M}\left(b^2 E + ab\beta - \frac{ad}{K}\beta - bcd - b^2 e\right). \end{array}$$

We observe that dz/dE is positive: even with increasing harvesting efforts on the predator z, its biomass increase. Also, dx/dE is positive implies increasing prey biomass. What seems to be counter-intuitive is that $dy/dE < 0$: the biomass of the first predator decreases when we harvest the second predator only. To see that the mathematics does not defy the ecology, consider that an increase in the biomass of the second predator implies an increase in the competition effect of the second predator on the first, i.e. $\alpha >> \beta$, as can be observed in the magnitude of $\frac{dy}{dE} = -(\frac{a}{K}\alpha + bc)$. As it is well know from the ecological principle of competitive extinction [4] when two competing species occupy the same niche, one of the two species, which is less competitive, will either get extinct or adapt to a new habitat. Hence, the behavior we obtained in this case is in accordance with this ecological principle and as long as the catfish biomass is increasing, we can not expect increase in the biomass of the striped bass. Such an adverse effect of the generalist predator invasive non-native catfish on the in the Chesapeake Bay could also justify why "although the striped bass stock is not overfished and overfishing is not occurring according model projections [spawning stock biomass] could fall below the threshold in the future” [6].

The second counter intuitive result is the increase in the biomass of the second predator, the catfish, even though it is harvested. This result however does not contradict our previous findings in [11], where we have shown that only with a very aggressive harvesting of the catfish such that the harvesting effort (h) is comparable or greater that the intrinsic growth rate of the catfish ($h \geq e$) its growth could be controlled. Such aggressive harvesting resulted in a phase-shifted behavior of the catfish and the prey, and on a long run the striped bass still got extinct supporting the principle of competitive extinction. Furthermore, since $dz/dE > 0$, it follows that the quadratic yield function $Y(E) = Ez(E)$ will not have a maximum value and hence the harvesting of the catfish only could be done at any level but will still not be sufficient to halt its invasive effect.

When harvesting the catfish only, as shown in Figure 6, we see that biomass of both catfish and menhaden is increasing as the effort increases, while the biomass of the bass is decreasing. Furthermore, MSY can not be attained due to the fact that yield is constantly increasing. Hence, in order to avoid the danger of driving the striped bass to extinction, harvesting the catfish only must be halted at some point.

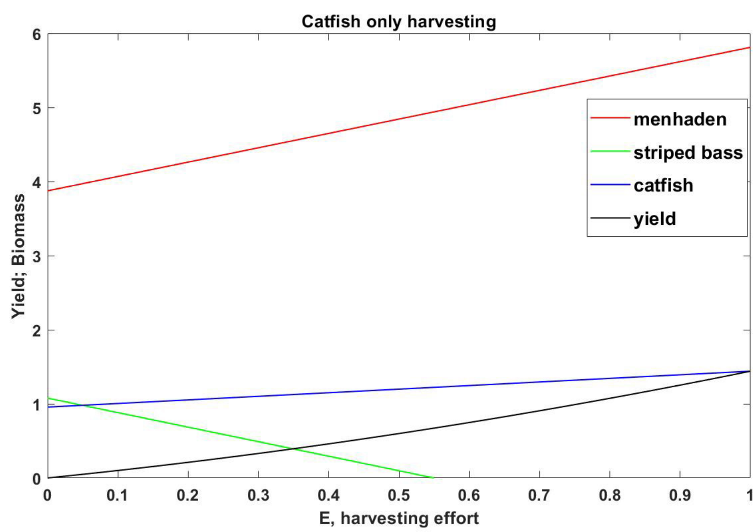


Figure 6: Yield and the three species biomass as a function of the harvesting effort when harvesting the catfish only. Parameters values are as follows: $K = 5, a = 1, b = 0.2, c = 0.01, d = 0.01, e = 0.5, \alpha = 0.8$, and $\beta = 0.5$.

Combined harvesting.

In this case, let us assume that $E_1 = E_2 = E_3 = E \neq 0$. Solving for x, y, z as a function of E, we obtain

$$\begin{aligned} x(E) &= \tfrac{1}{M}\left((c\beta - \alpha\beta + b\alpha)E + cd\beta + a\alpha\beta - be\alpha\right) \\ y(E) &= \tfrac{1}{M}\left((-bc + c^2 - \tfrac{a}{K} - c\alpha)E + ac\alpha + bce + c^2 d + \tfrac{a}{K}e\alpha\right) \\ z(E) &= \tfrac{1}{M}\left((b^2 - bc - \tfrac{a}{K}\beta - b\beta)E + ab\beta - \tfrac{ad}{K}\beta - bcd - b^2 e\right), \end{aligned} \tag{3.6}$$

where $M = \frac{a}{K}\alpha\beta + bc(\alpha + \beta)$. Observe that among the three, only $y(0)$ is guaranteed to be positive. We consider the situation where $\frac{dx}{dE}, \frac{dy}{dE}, \frac{dz}{dE}$ are all negative; in this case, the biomass of the species decrease when combined harvesting effort increases. The goal is to find conditions so that none of the species become extinct. Also, the biologically relevant scenario is when the $x(0), y(0), z(0) > 0$.

The yield function is

$$Y(E) = E(x(E) + y(E) + z(E)).$$

Since we assumed that $\frac{dx}{dE}, \frac{dy}{dE}, \frac{dz}{dE}$ are all negative, it follows that the quadratic function $Y(E)$ has a maximum yield value, which is attained when the effort is equal to

$$E^* = \frac{-(x(0) + y(0) + z(0))}{2(m_x + m_y + m_z)}.$$

Denote

$$E_x^* = \frac{-x(0)}{m_x}, \;\; E_y^* = \frac{-y(0)}{m_y}, E_z^* = \frac{-z(0)}{m_z},$$

where $m_x = \frac{dx}{dE}$, $m_y = \frac{dy}{dE}$, and $m_z = \frac{dz}{dE}$.

Theorem 3.4. *Using (3.6), assume that*

1. $\frac{dx}{dE}, \frac{dy}{dE}, \frac{dz}{dE} < 0$
2. $x(0), z(0) > 0$.

When harvesting all three species with the same effort, maximum sustainable yield is achieved, provided,

$$E^* < \min\{E_x^*, E_y^*, E_z^*\}.$$

Using the same values for the model's parameters as before, we graph the yield and the biomass of the three fish species when the harvesting effort is applied to all three species as shown in Figure 7. As expected from the theoretical results, the biomass of all three fish is decreasing as the effort increases. We can also see that in this particular case, even though $E^* < E_x^*, E_y^*, E_z^*$, and hence the system is sustainable, the biomass of the both predators is getting critically low which will be too detrimental to their long term sustainability.

Student Exploration Activity. In the analyses presented when harvesting predators only, it is assumed that the harvesting efforts E_1 and E_2 are equal. Analogously, when harvesting all three species, it is assumed that $E_1 = E_2 = E_3$ (which is why the case is called *combined harvesting*). Consider the case when harvesting efforts are not equal. In these cases, what are the corresponding yield functions? Geometrically, what kind of graphs will aid analyses of these cases?

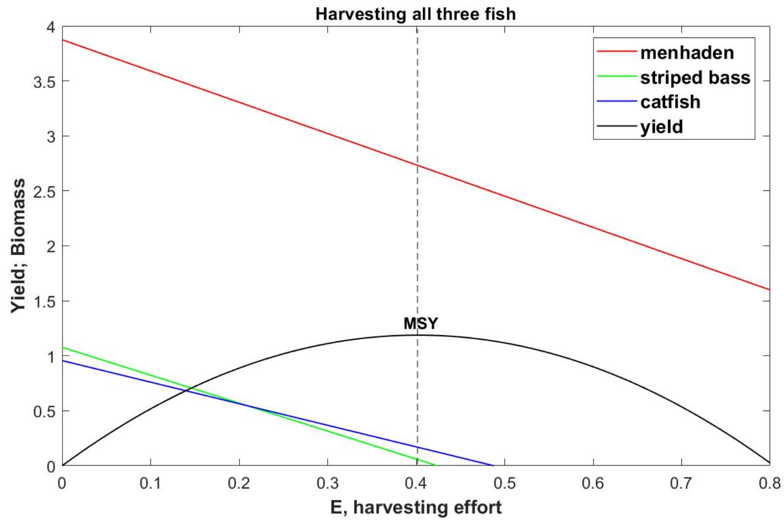


Figure 7: Yield and the three species biomass as a function of the harvesting effort when harvesting all three species. Parameters values are as follows: $K = 5, a = 1, b = 0.2, c = 0.01, d = 0.01, e = 0.5, \alpha = 0.8$, and $\beta = 0.5$.

4 Balancing the Economic and Ecological Harvesting Goals

At this point, it is natural to ask how are the results on the bionomic equilibrium related to the results on the maximum sustainable yield? Observe that the computations in Section 2 involve specific points $P(x_B, y_B, z_B, E_1, E_2, E_3)$ while computations in Section 3 involve functions $x(E), y(E), z(E)$ on the effort E. While Section 2 tackles the analysis of the economic structure via the total net revenue $\pi(E)$ as a function of harvesting, Section 3 considers the investigation of a very important ecological issue, extinction, as a function of harvesting. In this section, we address the problem of relating these economic and ecological considerations, in particular, at what harvesting efforts are we able to maintain the ecological and economic structures of our system?

Let us look at the case when we harvest the prey only, that is, $E_1 = E \neq 0$ with $E_2 = E_3 = 0$. Analysis of the other cases follows analogous arguments.

Consider the overall net revenue when $E_2 = E_3 = 0$ from Case 6 (B) in Section 2 and express it in terms of the yield $Y(E)$:

$$\pi(E) = (p_1 x(E) - c_1)E = p_1 x(E)E - c_1 E = p_1 Y(E) - c_1 E. \tag{4.1}$$

Oftentimes, this overall net revenue function in Economics is also called the profit because $p_1 Y(E)$ gives the revenue (money coming in due to harvesting E) while $c_1 E$ gives the cost (money coming out due to harvesting E). In the table in Table 3 (for simplicity we set the harvesting coefficient $q_1 = 1$), we see that $\pi(E_1) = 0$ where,

$$E_1 = a\left(1 - \frac{x_B}{K}\right) - by_B - cz_B, \tag{4.2}$$

with $(x_B, y_B, z_B) = (\frac{c_1}{p_1}, \frac{1}{\beta}(e + cx_B), \frac{1}{\alpha}(-d + bx_B))$. Let us seek the maximum of the profit function $\pi(E)$; computing the derivative, we have

$$\pi'(E) = p_1 Y'(E) - c_1 = p_1(x(E) + x'(E)E) - c_1.$$

From Section 3, we know that the biomass $x(E)$ of the prey is a linear function of E, that is, $x(E) = m_x E + x(0)$ so that $\pi'(E) = 0$ if and only if $p_1(m_x E + x(0) + m_x E) - c_1 = 0$, i.e.,

$$\bar{E} = \frac{c_1}{2p_1 m_x} - \frac{x(0)}{2m_x}. \tag{4.3}$$

Since $\pi''(E) < 0$ for all E because $m_x < 0$ in the case when we harvest prey only, we see that π achieves a maximum at the effort $\bar{E}$. In this case, we say that $\bar{E}$ gives us the maximum economic yield (MEY).

We then ask, how does the MEY relate to the MSY when we harvest the prey only? Recall that the harvesting effort to achieve MSY when harvesting prey only is given by

$$E^* = \frac{-x(0)}{2m_x}, \tag{4.4}$$

so that using (4.3), it follows that

$$\bar{E} = \frac{c_1}{2p_1 m_x} + E^* < E^*,$$

because $m_x < 0$. To complete our analysis, we next investigate the bionomic equilibrium effort E_1 (4.2) in relation to the MEY (4.3) and the MSY (4.4). Since $\pi(E_1) = 0$, it follows from (4.1) that

$$p_1 x(E_1) - c_1 = 0 \Longrightarrow x(E_1) = \frac{c_1}{p_1} = x_B.$$

In other words, the x-coordinate of the bionomic equilibrium in case we harvest the prey only is just one point on the linear function $x(E)$, that is, the point (E_1, x_B) lies on the graph of the line $x(E)$ and the vertical line where $E = E_1$. Moreover, we have that

$$\frac{c_1}{p_1} = x(E_1) = m_x E_1 + x(0) \Longrightarrow E_1 = \frac{c_1}{p_1 m_x} - \frac{x(0)}{m_x}.$$

We have to consider two cases: $x_B < \frac{x(0)}{2}$ and $x_B > \frac{x(0)}{2}$. In the first case, we have that

$$E_1 - E^* = \frac{c_1}{p_1 m_x} - \frac{x(0)}{2m_x} > 0 \Longrightarrow E^* < E_1.$$

In the second case, we have that $E_1 < E^*$. Let us summarize our results into a theorem:

Theorem 4.1. *Assume that harvesting efforts are implemented on the prey only. Furthermore, suppose*

1. *The bionomic equilibrium $P(x_B, y_B, z_B, E_1, 0, 0)$ exists where harvesting effort E_1 is given in (4.2);*

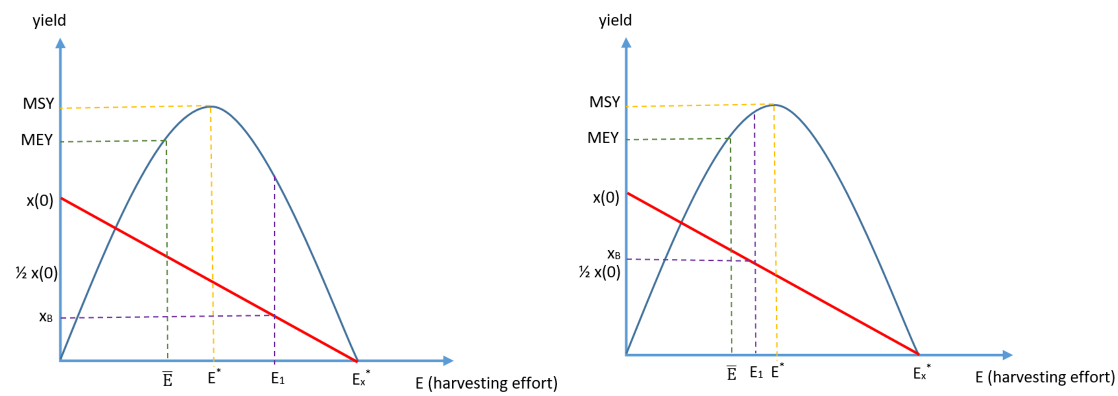
2. *the maximum economic yield is achieved at the effort $\bar{E}$ where $\bar{E}$ is given in (4.3); and*

3. the maximum sustainable yield is achieved at the effort E^* where E^* is given in (4.4).

Then

- *If $2x_B < x(0)$, we have that $\bar{E} < E^* < E_1$.*
- *If $2x_B > x(0)$, we have that $\bar{E} < E_1 < E^*$.*

In particular, the maximum economic yield can always be achieved at harvesting efforts that are less than the efforts to reach maximum sustainable yield. Moreover, if $x_B > x(0)/2$, that is, the ratio of the cost per unit effort to the price per unit biomass is more than half of the biomass when no harvesting of prey is implemented, then harvesting efforts that exceed $\bar{E}$ may lead to a zero profit even before maximum sustainable yield is achieved. In other words, from both the economic and ecological sense, it does not make sense to harvest more fish when doing so becomes more costly.



(a) Case 1: $\bar{E} < E^* < E_1$

(b) Case 2: $\bar{E} < E_1 < E^*$

Figure 8: Relationship between the harvesting efforts $\bar{E}$ for maximum economic yield, E^* for maximum sustainable yield, and the effort E_1 to achieve bionomic equilibrium.

Student Exploration Activity. Consider Figures 2 and 8. Create a graph that combines the two graphs in one coordinate system.

1. The intersection of the lines $x = x(E)$ and $E = E_1$ is x_B. Where is y_B? How about z_B? Identify these points in your combined graph.
2. When the harvesting effort is $E = \bar{E}$, which achieves MEY, compute the corresponding biomasses for the three species, that is, what are $x(\bar{E})$, $y(\bar{E})$, and $z(\bar{E})$? Describe how to visualize these three points using the combined graph that you created.
3. When the harvesting effort is $E = E^*$, which achieves MSY, compute the corresponding biomasses for the three species, that is, what are $x(E^*)$, $y(E^*)$, and $z(E^*)$? Describe how to visualize these three points using the combined graph that you created.

5 Conclusion

Mathematical modeling is a powerful tool that can be used for understanding the behavior of real-world systems. Here we used mathematical modeling to study the dynamics of two predators and one prey system in the Chesapeake Bay and considering the seemingly contradicting goals of the fishermen (gain profit) and the ecosystem (avoid extinction). This work could be used as an individual or group project in a mathematical modeling class. As mathematics is sometimes seen as a solitary activity, assigning group mathematical modeling projects encourage students to work together and will emphasize that modeling is an inherently collaborative process. Moreover, this project highlights an interdisciplinary approach towards solving a real-life issue by weaving mathematical concepts such as differential equations, equilibrium points and graphs of parabolas and lines with economical concepts such as maximum yield, maximum profit, and economic equilibria.

As most fisheries management focus on yield maximization (higher profit for fishermen, more jobs, increased food security), it is very important to understand the long-term effects of such a policy on sustainability of the species population. Here we use one prey (Atlantic menhaden) and two competing predators (striped bass and the invasive catfish) model to investigate the impact of maximum sustainable yield policy. We have shown that harvesting the prey only at MSY level under certain conditions on the model's parameters may result in extinction of one or even both predators; while harvesting the predators at MSY levels is beneficial for the prey as their biomass is increasing as the harvesting effort increases. We have also shown that harvesting both predators, the native striped bass and the invasive catfish, at MSY level is sustainable and while the biomass of the striped bass is decreasing with the increased effort, the biomass of the catfish could decrease or increase depending on the model parameters. Another interesting, but unexpected result of this study was obtained in the case when the harvesting effort was applied only on the catfish, and even though the other predator was not harvested, its biomass was still decreasing with increasing the effort on the catfish. Even though these results may seem puzzling, they are in compliance with the well known principle of competitive exclusion [4] that if two competing species occupy the same niche in an ecosystem, they cannot co-exist indefinitely, one will either get extinct or will adapt to fill a different niche of the ecosystem. In conclusion, our study showed that even a very aggressive harvesting will not be sufficient to halt the invasive effects of the non-native catfish in the Chesapeake Bay area and some other approaches may be needed in order to reduce their intrinsic growth rate.

Finally, the mathematics and economics computations in the final section provide evidence that when harvesting prey only, efforts to achieve maximum economic yield (MEY) is less than the harvesting efforts to achieve MSY. In other words, fishing beyond efforts that yield MEY will not guarantee more economic returns but will require more costs (jobs, fishing boats, fuel). Moreover, it is even possible that fishing beyond efforts that yield MEY may lead to an effort E_1 that yields zero overall net revenue when harvesting prey only.

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